

# **Aspects of the Biology and Ecology of Six Temperate Reef Fishes (Families: Labridae and Monacanthidae)**

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Submitted in fulfillment of the requirements for the degree of Doctor of Philosophy,  
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## **Statements**

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## Abstract

The currently most accepted population theory for reef fish was developed on tropical reefs and suggests that populations of most reef fish species are limited primarily by recruitment, with little post-recruitment resource limitation. I tested the validity of this theory for temperate reef fishes by examining growth rates in six common species from a number of isolated populations for evidence of resource limitation. If resources are limiting, spatial and temporal variation in recruitment and mortality should lead to isolated populations experiencing differing levels of resource availability, particularly food availability, which will be reflected in growth rates. I worked with six of the most common reef fishes found in Tasmanian waters so that any findings would form the basis of a broadly applicable model. These were *Notolabrus tetricus*, *Notolabrus fucicola*, *Pictilabrus laticlavius*, *Pseudolabrus psittaculus*, *Penicipelta vittiger*, and *Meuschenia australis*.

Before examining growth rates it was first necessary to define the scale at which populations could be considered to be isolated. The short and long-term movement patterns of each species were studied using visual observations to interpret short-term patterns, and recaptures of tagged fish to interpret the long-term patterns.

Methods of ageing each species were developed and validated, with growth rates of tagged fish being used to validate the use of otoliths for ageing. General growth curves are presented.

For most of the species, there was some uncertainty in current texts about the sexual system used and the relationship between sex and dichromatism and dimorphism. To clarify this situation the reproductive biology of each species was examined. The relationship between sex and growth rate was also examined.

For two species (*N. tetricus* and *N. fucicola*) annual growth data from tagged fish were obtained over a 3-4 year period, allowing inter-annual growth variability to be examined. As well as providing an insight into the variability of growth with time, these results also aid in the interpretation of growth curves determined from otolith ageing.

In all species investigated, no significant differences in growth rates were detected between populations occupying similar habitats and subject to similar environmental conditions. These results suggest that post-recruitment resource limitation in the form of food limitation may not be an important factor influencing the post recruitment growth and survival of many temperate reef fishes with pelagic larval stages. This agrees with the assumptions made, but rarely tested, in current theories concerning the regulation of populations of reef fish, particularly those on temperate reefs.

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# Table of Contents

<b>1</b>	<b>Introduction</b>	
1.1	General	01
1.2	The model species	07
1.2.1	<i>Notolabrus tetricus</i>	07
1.2.2	<i>Notolabrus fucicola</i>	07
1.2.3	<i>Pictilabrus laticlavus</i>	07
1.2.4	<i>Pseudolabrus psittaculus</i>	08
1.2.5	<i>Penicipelta vittiger</i>	08
1.2.6	<i>Meuschenia australis</i>	09
<b>2</b>	<b>Movement</b>	
2.1	Introduction	10
2.1.1	General	10
2.1.2	Aims	11
2.2	Materials and methods	12
2.2.1	Study sites and species	12
2.2.2	Short-term movements and observations	12
2.2.3	Long-term movements	14
2.3	Results	17
2.3.1	Short-term movements	17
2.3.1.1	<i>Notolabrus tetricus</i>	17
2.3.1.2	<i>Notolabrus fucicola</i>	18
2.3.1.3	<i>Pictilabrus laticlavus</i>	18
2.3.1.4	<i>Pseudolabrus psittaculus</i>	19
2.3.1.5	<i>Penicipelta vittiger</i>	19
2.3.1.6	<i>Meuschenia australis</i>	19
2.3.2	Long-term movements	20
2.4	Discussion	27
<b>3</b>	<b>Growth</b>	
3.1	Introduction	31
3.2	Materials and methods	32
3.2.1	Tag-based growth estimates	32
3.2.1.1	Site and sampling details	32
3.2.1.2	Analysis of growth	32

3.2.2	Otolith and scale based growth estimates	33
3.2.2.1	Sites and collection methods	33
3.2.2.2	Analysis	34
3.2.3	Validation	35
3.3	Results	36
3.3.1	<i>Notolabrus tetricus</i>	36
3.3.1.1	Tag based growth estimates	36
3.3.1.2	Otolith based growth estimates	39
3.3.1.3	Validation	40
3.3.2	<i>Notolabrus fucicola</i>	42
3.3.2.1	Tag based growth estimates	42
3.3.2.2	Otolith based growth estimates	44
3.3.2.3	Validation	47
3.3.2.4	Sex related growth	48
3.3.3	<i>Pictilabrus laticlavius</i>	49
3.3.3.1	Tag based growth estimates	49
3.3.3.2	Otolith based growth estimates	51
3.3.3.3	Validation	55
3.3.4	<i>Pseudolabrus psittaculus</i>	56
3.3.4.1	Tag based growth estimates	56
3.3.4.2	Otolith based growth estimates	58
3.3.4.3	Validation	60
3.3.5	<i>Penicipelta vittiger</i>	61
3.3.5.1	Introduction	61
3.3.5.2	Males	63
3.3.5.2.1	Tag based growth estimates	63
3.3.5.2.2	Otolith based growth estimates	64
3.3.5.2.3	Validation	66
3.3.5.3	Females	66
3.3.5.3.1	Tag based growth estimates	66
3.3.5.3.2	Otolith based growth estimates	68
3.3.5.3.3	Validation	68
3.3.6	<i>Meuschenia australis</i>	69
3.3.6.1	Introduction	69
3.3.6.2	Males	70
3.3.6.2.1	Tag based growth estimates	70
3.3.6.2.2	Otolith based growth estimates	70
3.3.6.2.3	Validation	74
3.3.6.3	Females	76



3.3.6.3.1	Tag based growth estimates	76
3.3.6.3.2	Otolith based growth estimates	76
3.3.6.3.3	Validation	79
3.4	Discussion	81
3.4.1	Validation	81
3.4.2	Individual growth variability	83
3.4.3	Labrid growth	85
3.4.4	Monacanthid growth	86
<b>4</b>	<b>Reproduction</b>	
4.1	Introduction	88
4.1.1	General	88
4.1.2	Labrid reproductive biology	88
4.1.3	Monacanthid reproductive biology	90
4.1.4	The Tasmanian species	91
4.1.5	Aim	92
4.2	Materials and methods	92
4.2.1	Collection sites and methods	92
4.2.2	Analysis	93
4.3	Results	95
4.3.1	<i>Notolabrus tetricus</i>	95
4.3.1.1	Sexual system	95
4.3.1.2	Histology	97
4.3.1.3	Spawning duration	100
4.3.1.4	Reproductive behaviour	100
4.3.2	<i>Notolabrus fucicola</i>	101
4.3.2.1	Sexual system	101
4.3.2.2	Histology	104
4.3.2.3	Spawning duration	104
4.3.2.4	Reproductive behaviour	104
4.3.3	<i>Pictilabrus laticlavius</i>	105
4.3.3.1	Sexual system	105
4.3.3.2	Histology	108
4.3.3.3	Reproductive behaviour	110
4.3.4	<i>Pseudolabrus psittaculus</i>	110
4.3.4.1	Sexual system	110
4.3.4.2	Histology	112

4.3.4.3	Reproductive behaviour	112
4.3.5	<i>Penicipelta vittiger</i>	114
4.3.5.1	Sexual system	114
4.3.5.2	Reproductive behaviour	118
4.3.6	<i>Meuschenia australis</i>	118
4.3.6.1	Sexual system	118
4.3.6.2	Reproductive behaviour	120
4.4	Discussion	121
4.4.1	Spawning	121
4.4.2	Labrid sexual systems	123
4.4.3	Monacanthid sexual systems	126
<b>5</b>	<b>Interannual variation in growth</b>	<b>127</b>
5.1	Introduction	127
5.2	Materials and methods	129
5.3	Results	130
5.3.1	<i>Notolabrus fucicola</i>	130
5.3.2	<i>Notolabrus tetricus</i>	133
5.4	Discussion	137
<b>6</b>	<b>Spatial patterns of growth</b>	<b>141</b>
6.1	Introduction	141
6.2	Materials and Methods	148
6.2.1	Species and Collections	148
6.2.2	Collection methods and procedures	149
6.2.3	Analysis	150
6.3	Results	151
6.3.1	Variation in growth between sites with similar habitats	151
6.3.1.1	<i>Notolabrus tetricus</i>	151
6.3.1.2	<i>Notolabrus fucicola</i>	154
6.3.1.3	<i>Pictilabrus laticlavius</i> and <i>Pseudolabrus psittaculus</i>	156
6.3.1.4	<i>Penicipelta vittiger</i>	156
6.3.1.5	<i>Meuschenia australis</i>	158
6.3.2	Variation in growth between different habitats	160
6.3.2.1	<i>Notolabrus tetricus</i>	160
6.3.2.2	<i>Notolabrus fucicola</i>	161
6.3.2.3	<i>Pictilabrus laticlavius</i>	162
6.3.2.4	<i>Pseudolabrus psittaculus</i>	162

6.3.2.5	<i>Penicipelta vittiger</i>	163
6.3.2.6	<i>Meuschenia australis</i>	164
6.4	Discussion	164
6.4.1	Growth in similar habitats	164
6.4.2	Growth in different habitats	166
6.4.3	General discussion	168
<b>7</b>	<b>Concluding Discussion</b>	<b>172</b>
7.1	Introduction	172
7.2	Movement	172
7.3	Age and growth	174
7.4	Reproduction	176
7.5	Spatial variability in growth	178
<b>References</b>		<b>182</b>

# **Chapter 1 Introduction**

## **1.1 General**

In Australia, and in fact worldwide, the impacts that humans have exerted on populations and assemblages of temperate reef fishes are only just beginning to be recognised, impacts that have been caused by mechanisms such as exploitation, pollution, and habitat modification (Lincoln-Smith and Jones 1995). With this recognition has come the realisation that our knowledge of the biology and ecology of most of the impacted species is very limited, and that research for both fisheries management and conservation purposes is urgently needed. This paucity of research has occurred for two principle reasons. Firstly, reef based fisheries are generally small and target a range of species, producing low economic returns. Often in such fisheries, the costs of research and management can outweigh the value of the fishery (Russ 1991). Therefore, fisheries management authorities and funding bodies have largely ignored this area of research, in preference for the major fisheries based on pelagic and demersal species which provide substantially greater economic returns. The second reason for the absence of temperate research, is that most reef fish ecologists prefer to work in tropical waters due to the substantial advantages that these offer over temperate waters (Sale 1980, Ebeling and Hixon 1991). These advantages include calmer working conditions, greater visibility, warmer temperatures enabling longer dive times and improved diver comfort, and the opportunity for greater experimental replication that is offered on coral reefs due to the occurrence of isolated coral heads and patch reefs.

While research on temperate reef fishes has been limited, and is the subject of only a few specific reviews (e.g. Choat 1982, Jones 1988), there is now an extensive literature on the biology and ecology of tropical reef fishes, much of which has been recently reviewed in Sale (1991) by a number of authors, or is the subject of other more specific texts and reviews (e.g. Ehrlich 1975, Sale 1980, Thresher 1984, Doherty and Williams 1988a). In addition, much is now known about the effectiveness of tropical marine

reserves (Roberts and Polunin 1991), and the management of tropical reef fisheries (Polunin and Roberts 1995). A substantial proportion of the knowledge gained from tropical studies, particularly in the area of population regulation, could be directly applicable to temperate regions. However, in a recent comparison of the published information on community structure of tropical and temperate reef fishes, Ebeling and Hixon (1991) concluded that there were, at that time, too few studies available from temperate reefs to assess the universality of community regulation models developed from tropical studies, particularly given the real differences that exist between temperate and tropical reef fish communities at a descriptive level.

Some of the more recently published studies examining long-term changes in assemblage structure in both temperate (Holbrook *et al.* 1995) and tropical (Sale *et al.* 1994) reef fishes suggest that there may be some congruence in the patterns operating at the assemblage level, as the relative composition and abundance of most constituent species are highly variable. However, it is not yet clear as to whether these patterns are caused by the same processes. For coral reef assemblages, at least for the majority of species which have an open reproductive system with a dispersive larval phase, there is an increasing amount of evidence suggesting that the strongest process structuring assemblages is temporal variability in the availability of new recruits from the plankton (Doherty and Williams 1988a, 1988b, Doherty and Fowler 1994). However, while recruitment limitation is emerging as an important structuring process, studies have also shown that, at least occasionally, recruitment is sufficient for resource limitation to occur, with density dependant processes then becoming more important (Jones 1987a). More research is needed to determine how frequently recruitment strength in most species is sufficient for post-recruitment processes to become important. For species with closed reproductive systems, recruitment is probably rarely limiting, and in such species resource limitation is likely to be the most important process structuring populations (Thresher 1983, 1985).

In temperate waters, the vast majority of research on population regulation has been fisheries based rather than reef based, and has been focussed on commercial pelagic and demersal species. This work has shown that many species undergo large changes in population size between years which is primarily mediated by interannual variability in larval mortality (Cushing 1975). This situation closely parallels that now reported in tropical reef fishes (Doherty and Williams 1988a), and suggests that there may be some similarity between the processes structuring populations for many tropical reef fishes and commercially exploited temperate pelagic and demersal fishes.

Due to a lack of research much less is known of the mechanisms regulating population size for temperate reef fishes. While it is possible that these mechanisms will be similar to those operating on tropical reefs and in temperate commercial species, preliminary studies have had conflicting results. For example, Stephens and Zerba (1981), who examined many species in an assemblage of reef fishes, found no evidence of resource limitation, while Jones (1984b) reported that resource limitation substantially influenced growth rates and time to maturity in *Pseudolabrus celidotus*. Resource limitation has also been reported in the temperate surfperch *Embiotoca jacksoni* and *E. lateralis* (Holbrook and Schmitt 1986; Schmitt and Holbrook 1990). However, resource limitation would be expected in these species as both have a closed, rather than open, reproductive system, giving birth to live young which remain on the parental reef.

If the impacts of fishing, pollution and habitat loss are to be properly assessed on temperate reefs, far more work needs to be directed at understanding the processes regulating assemblages of fishes on them, and identifying any parallels that occur between temperate and tropical reefs. Some of the most important questions that need to be answered include the following.

(1) Are assemblages of temperate reef fishes primarily limited by recruitment or by resource availability?

- (2) If recruitment is important, what are the processes that influence recruitment success?
- (3) If resource limitation is important then what resources are limiting (food, space, shelter)?
- (4) Is there a stock recruitment relationship operating for most species in most years?

As reef-based fisheries target a range of species using the same or similar fishing methods, the management problems associated with such fisheries represent a particularly substantial challenge to fisheries managers (Roberts and Polunin 1991, Russ 1991). This is because of the interactive nature of this type of fishery where, although one target species may be particularly well managed through appropriate research and a sustainable catch limit, the many other species that are caught as a by-catch may be accidentally overexploited. These problems may be eventually overcome when the biology and ecology of all exploited species is fully understood, and appropriate management strategies are implemented. However such an outcome is not likely in the immediate future given the present level of funding and research priorities of fisheries authorities (Russ 1991).

An alternative and parallel approach to this management problem may be the establishment of networks of marine reserve areas closed to fishing. This alternative approach to protecting a breeding population capable of supplying new recruits to adjacent areas has been widely advocated (e.g. Wallis 1971; Ballantine 1991; Bohnsack 1990). As well as providing a valuable management solution, this strategy also acts as insurance against the collapse of fisheries managed by traditional methods. It also enables the conservation of marine communities in their natural state and significantly aids scientific research by allowing assessment of the impacts of fishing in adjacent areas by comparison with levels of unexploited stocks in reserves. The vast majority of marine reserves established so far have been in tropical regions and, therefore, marine reserve research has mostly been concentrated in these regions. The results of research

into the effectiveness of tropical marine reserves has been reviewed by Roberts and Polunin (1991). The major findings of this review were that the average size and abundance of many large carnivorous fishes were enhanced by the reserves, but nothing was yet known of the rates of immigration or emigration to reserves, or of the contribution that recruits supplied by breeding stocks in reserves make to adjacent fished populations.

Understanding the role that movements can play in the effectiveness of reserves is an essential pre-requisite for the design of such reserves. As research into spiny lobster *Jasus edwardsii* populations in the Cape Rodney to Okakari Point Marine Reserve in temperate New Zealand has shown, lobster numbers and size increased significantly compared to adjacent areas after the reserve was established. However, small offshore movements by male lobsters resulted in them emigrating outside the reserve boundaries where they were targeted by local fishermen (MacDiarmid and Breen 1992). If the aim of a reserve is to contain and protect breeding populations of reef fishes, then the movement patterns of the species to be protected need to be fully understood, so that reserve size and boundaries can be chosen to minimise losses.

The major aim of the research presented in this thesis is to examine the applicability of population regulation models, developed on tropical reefs, to temperate reef fish assemblages. This work also has two important secondary aims, of firstly providing information on fish movements that may be valuable in the design of more effective marine reserves, and secondly expanding the extremely limited knowledge of the biology of some of southern Australia's most common reef fishes.

The particular focus of the primary aim was to test the assumption of Doherty and Williams (1988a, 1988b) recruitment-limitation model, that most natural reef fish populations are rarely resource limited. This was done by examining the extent to which natural populations are limited for those resources which determine growth rates. Jones



(1984b) found that isolated populations of the temperate reef fish *Pseudolabrus celidotus*, occurring in similar habitats, could have substantially different rates of growth and times to maturity, presumably as a result of greater food limitation in areas of high recruitment or survivorship. As this result was counter to that predicted by Doherty and Williams (1988a, 1988b), it is important to examine whether the results of Jones (1984b) were more widely applicable to temperate reef fishes, or are atypical. To do this, I chose to work with six of the most common reef fishes found in Tasmanian and southern Australian waters as model species, examining the extent to which growth varied between isolated populations occupying similar habitats, but which were presumably subject to different rates of recruitment and mortality, and therefore to different levels of resource availability which could influence growth.

Before this could be done, it was first necessary to examine the extent of movements of the model species, so that the scale at which populations could be considered to be isolated was identified. Also, growth had to be studied in each species, and the ageing techniques used to examine growth had to be validated. Because growth rates may be sexually specific, it was also necessary to examine the sexual systems of each species, and to determine any relationship between sex and morphology that would enable easy identification of the sexes.

Particular emphasis was placed on the movement patterns of the model species because of the implications that these movements have for the effective design of marine reserves, specifically the minimum size that individual reserves should be, and the type of boundaries that may be effective in constraining emigration. As the species chosen for this study were amongst the most common on Tasmanian reefs, they represented an appropriate choice for studying the effectiveness of reserves in Tasmanian waters at protecting representative assemblages of reef fishes.

## 1.2 The model species

The six model species consisted of four labrids (*Notolabrus tetricus*, *N. fucicola*, *Pictilabrus laticlavius*, and *Pseudolabrus psittaculus*) and two monacanthids (*Penicipelta vittiger*, and *Meuschenia australis*), representing two of the most common families found in southern Australian waters. The distribution of each species includes all Tasmanian waters with suitable habitat. The nomenclature for the labrids follows the review of Russell (1988), while that for the monacanthids follows Last *et al.* (1983).

1.2.1 *Notolabrus tetricus*: Commonly called the bluethroated wrasse, or bluehead parrotfish, this species was first described as *Labrus tetricus* by Richardson (1840) from a type specimen collected in Port Arthur, Tasmania. It has been known as *Pseudolabrus tetricus*, and was only recently placed in the genus *Notolabrus* by Russell (1988). Its distribution is from Sydney (N.S.W.) to Spencer Gulf (S.A.), and it occurs on both sheltered and exposed reefs from 0 to 40 m, although generally in the deeper waters on exposed reefs. In Tasmanian waters this species grows to 500 mm, and the diet is predominantly molluscs, echinoids and crustaceans, particularly decapod crustaceans (Edmunds 1990).

1.2.2 *Notolabrus fucicola*: Commonly called the purple wrasse, saddled wrasse, or kelpie, this species was first described as *Labrus fucicola* by Richardson (1840) from a type specimen again collected in Port Arthur, Tasmania. This species was previously known as *Pseudolabrus fucicola*, being only recently placed in the genus *Notolabrus* by Russell (1988). The species distribution is from southern New South Wales to Kangaroo Is. (S.A.), and it is usually found on exposed reefs in 0 to 15 m of water. This species grows to at least 450 mm in Tasmanian waters, and has a diet of crustaceans and molluscs (Edmunds 1990).

1.2.3 *Pictilabrus laticlavius*: This species is commonly called the senator wrasse, or senatorfish, and was first described as *Labrus laticlavius* by Richardson (1839) from a type specimen collected in Port Arthur, Tasmania. It has also been described as *Eupetrichthys gloveri* (Scott 1974). Its distribution is from Seal Rocks (N.S.W.) to the Houtman Abrolos Islands (W.A.), and is usually found in 0 to 20 m of water on sheltered to moderately exposed reefs. This species grows to 300 mm in Tasmanian waters, with a diet of molluscs and small crustaceans, particularly amphipods (Edmunds 1990).

1.2.4 *Pseudolabrus psittaculus*: This species is commonly called the rosy wrasse, and was first described as *Labrus psittaculus* by Richardson (1840) from a type specimen collected in Port Arthur, Tasmania. It has also been mistakenly identified as *P. miles* (Bloch and Schneider 1801), a closely related species found in New Zealand waters. This species is found from Sydney (N.S.W.) to King George's Sound (W.A.), and is found on reefs of all exposures, in 10 to 220 m of water. In Tasmanian waters, this species grows to 250 mm, and has a diet of small invertebrates, which are predominantly crustaceans, echinoderms, and molluscs (Edgar *et al.* 1982). It has also been observed cleaning ectoparasites from other reef species (pers. obs.).

1.2.5 *Penicipelta vittiger*: Commonly called the toothbrush leatherjacket, this species was first described as *Monacanthus vittiger* Castelnau 1873, from a specimen collected in St Vincent Gulf, South Australia. It was also described as *P. vittiger* in that year by Castelnau. In a recently published fish identification handbook, Gomon *et al.* (1994) placed this species in the genus *Acanthaluteres*, presumably due to its similarity to the closely related species *A. spilomelanurus*. The distribution of *P. vittiger* is from Coffs Harbour (N.S.W.) to Jurien Bay (W.A.), on exposed to semi-exposed coastal reefs of 0 to 55 m depth, although it is most commonly found in shallow water from 0 to 10 m. This species grows to 320 mm in Tasmanian waters, and has a diet of small invertebrates, particularly amphipods and epifaunal invertebrates such as hydrozoans

(Last 1983). Feeding on algal associated invertebrates results in incidental inclusion of algae of up to 40% of gut contents (Last 1983), and further research is needed to determine the extent to which this is digested.

1.2.6 *Meuschenia australis*: Commonly called the brownstriped, brownbanded, or southern leatherjacket, this species was first described as *Balistes australis* Donovan 1824, from a type specimen collected in Tasmania. The distribution of this species is from Wilsons Promontory (Vic.) to Robe (S.A.) and it is found on coastal reefs of all exposures, from 0 to 30 m. While quite common in Tasmanian waters, it is less common elsewhere. This species grows to 320 mm in Tasmanian waters, and feeds on benthic invertebrates, including molluscs, echinoids, hydrozoans and poriferans (Last 1983).

## **Chapter 2 Short and Long-Term Movement Patterns**

### **1.1 Introduction**

#### *2.1.1 General:*

Based on more than three decades of research involving numerous studies, the majority of species of tropical reef fish are now regarded as being sedentary in habit, with individuals usually remaining in association with small areas of reef for most of their life (Ehrlich 1975; Sale 1991). This conclusion is based on the results of tagging studies (e.g. Randall 1962; Bohnsack 1990; Recksiek *et al.* 1991), as well as direct observations made on individual fish using SCUBA (e.g. Bardach 1958; Clarke 1970; Reese 1973; Thresher 1979). The scale of the daily movements within the reef of these sedentary species, may range from several metres in a small territorial species (Sale 1971) to several kilometres in species involved in either cross-reef spawning migrations (Johannes 1978), or migration from sleeping to feeding sites (Hobson 1972). As well as differences between species, there can also be considerable intra-specific variation in range size, with home-ranges tending to increase in proportion to the size of individuals (Sale 1978) and in inverse proportion to habitat quality (Matthews 1990). Intra-specific behavioural factors may also significantly influence spatial relationships (Ogden and Buckman 1973).

The majority of temperate reef fishes may also be sedentary. However, few studies are available for direct parallels to be drawn between the movement patterns of fishes on temperate and coral reefs. This derives primarily from the difficulties associated with using SCUBA in colder waters with low visibility. From the limited number of temperate studies conducted so far, families of temperate reef fishes found during behavioural studies to have site-attached representatives include labrids (Jones 1984), cheilodactylids (Leum and Choat 1980) and pomacentrids (Clarke 1970; Moran and

Sale 1977; Norman and Jones 1984). In tagging studies, families in which some species have been found to display site-attachment include the scorpaenids (Matthews 1990), embiotocids, labrids and pomacentrids (Davis and Anderson 1989), and serranids (bass) (Davis and Anderson 1989; Parker 1990; Low and Waltz 1991). Davis and Anderson (1989) studied four common Californian reef fishes, selected from different families and trophic positions, and found that all were site-attached, indicating site-attachment may be common in temperate reef fishes, regardless of family or trophic position.

While many temperate species may be site-attached, several studies have suggested that the tendency for year-round residency may decrease with increasing latitude because, at least in some temperate regions, large seasonal variations in water temperature are experienced, forcing reef residents into deeper offshore waters to avoid environmental extremes (Parker 1990) or causing them to hide in a state of torpor during the coldest months (Olla *et al.* 1979).

#### 2.1.2 *Aims:*

The major aim of this study was to define the scale of movements of the six species whose biology is examined in the following chapters. This was necessary to delineate population boundaries, a parameter which is of particular importance for the research presented in Chapter 6 where growth rates are compared between populations separated by relatively small distances (2 to 50 km).

A further aim of this study was to extend the limited knowledge of short and long-term movement patterns of temperate reef fishes, as the movement patterns of even the most common southern Australian reef fishes have not been described. A final aim was to assess the ability of natural habitat boundaries to constrain such movements. An understanding of factors such as these is essential for the design of marine reserves on temperate reefs, as well as for proper management of fisheries targeting reef species.

The species selected for study include some of the most common fishes in southern Tasmanian waters, and include four species of labrids and two species of monacanthids.

## 2.2 Materials and Methods

### 2.2.1 Study sites and species:

The study was conducted on a reef of 1 ha surrounding Arch Rock in Southern Tasmania, Australia, and at an adjacent reef at Ninepin Point one km away (Fig. 2.1). The reef at Arch Rock extends from the intertidal to a depth of 7-10 m, with an average offshore extension of 20 m, and completely surrounds the island, which has a circumference of 320 m. This reef is isolated from the nearest adjacent reef by a 1 km stretch of sand, with an average depth of 15 m, which is bare during winter but colonised by red algae during spring and summer. The habitat at this site is characterised by the macroalgae *Durvillea potatorum* and *Lessonia corrugata* in the immediate sub-littoral zone, extending through *Macrocystis pyrifera*, *Ecklonia radiata*, and *Sargassum fallax* from 2-10 m, to a carpet of predominantly red algae at 10 m. Sea temperatures range from 8-18°C during the year.

At Ninepin Point the reef extends from the intertidal to a depth of 15 m immediately off the end of the point, and to approximately 5 m depth when more than 50 m away from the end. This is a large reef covering approximately 5 ha, with habitat characteristics similar to that described for Arch Rock.

The species studied (Table 2.1) were the bluethroat wrasse (*Notolabrus tetricus*), purple wrasse (*Notolabrus fucicola*), senator wrasse (*Pictilabrus laticlavus*), rosy wrasse (*Pseudolabrus psittaculus*), toothbrush leatherjacket (*Penicipelta vittiger*), and brown banded leatherjacket (*Meuschenia australis*). The labrids *N. tetricus* and *N. fucicola*, and the monacanthid *P. vittiger*, together constitute some of the most abundant shallow reef fish in Tasmanian waters, while *P. laticlavus* is abundant in sheltered waters.

### 2.2.2 Short-term movements and observations:

A grid 70 m x 25 m, divided into 5 m x 5 m squares, was established on the Arch Island reef by means of bricks and rope. This extended from the shoreline to the maximum



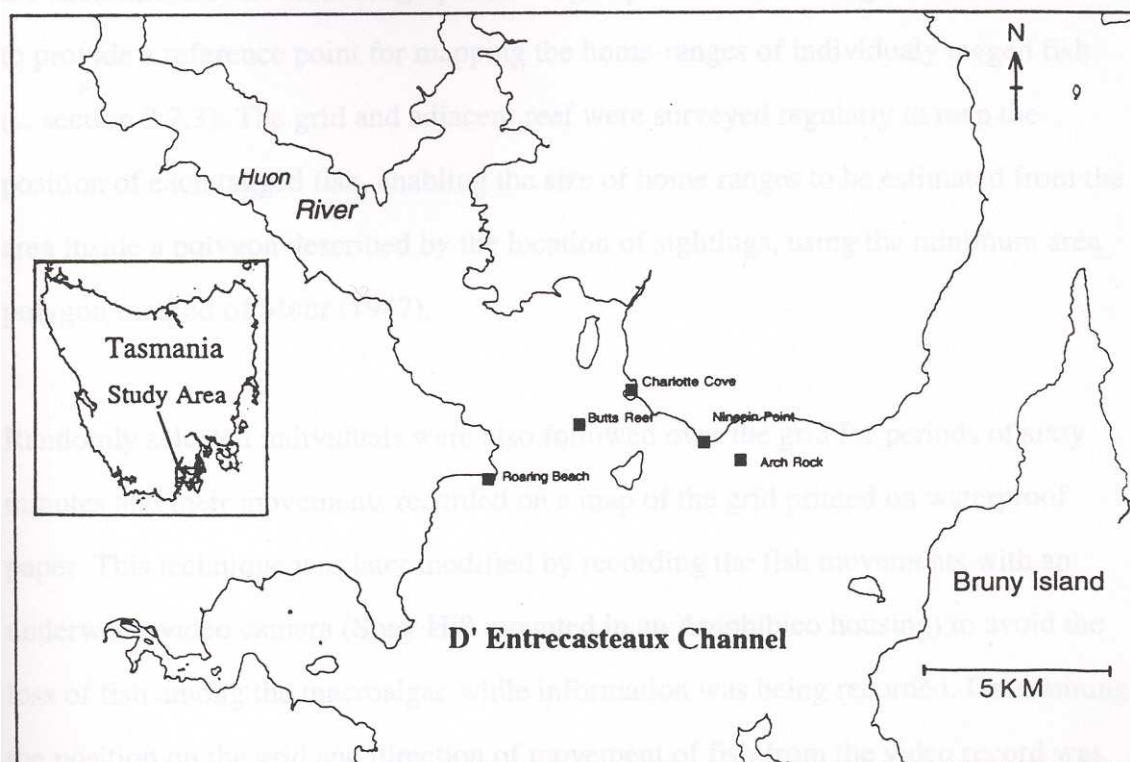


Figure 2.1. Lower D'Entrecasteaux Channel region of Tasmania, showing the location of the Arch Rock study site and Huon region fish collection sites.

Table 2.1. Biological characteristics of the species included in the Arch Rock movement study.

Family	Name	Max. length (cm)	Sexual system	Sexual dimorphism?	Sexually dichromatic?	Reference
Labridae	<i>Notolabrus tetricus</i>	45	Protogynous hermaphrodite	No	Yes	Russell (1988)
Labridae	<i>Notolabrus fucicola</i>	50	Gonochorism	No	No	Russell (1988)
Labridae	<i>Pictilabrus laticlavius</i>	30	Protogynous hermaphrodite	No	Yes	Russell (1988)
Labridae	<i>Pseudolabrus psittaculus</i>	25	Protogynous hermaphrodite	No	Yes	Last, <i>et al.</i> (1983)
Mona-canthidae	<i>Penicipelta vittiger</i>	32	Gonochorism	Yes	Yes	Last, <i>et al.</i> (1983)
Mona-canthidae	<i>Meuschenia australis</i>	30	Gonochorism	Yes	Yes	Last, <i>et al.</i> (1983)

offshore extension of the reef (20 m) and 5 m beyond, with one axis perpendicular to the shoreline and the other roughly following depth contours. The grid was established

to provide a reference point for mapping the home-ranges of individually tagged fish (v. section 2.2.3). The grid and adjacent reef were surveyed regularly to map the position of each tagged fish, enabling the size of home ranges to be estimated from the area inside a polygon described by the location of sightings, using the minimum area polygon method of Mohr (1947).

Randomly selected individuals were also followed over the grid for periods of sixty minutes and their movements recorded on a map of the grid printed on waterproof paper. This technique was later modified by recording the fish movements with an underwater video camera (Sony Hi8 mounted in an Amphibico housing) to avoid the loss of fish among the macroalgae while information was being recorded. Determining the position on the grid and direction of movement of fish from the video record was simple, as the position could be identified from distinguishing features on the reef, and the slope of the reef was sufficient to differentiate which axis of the grid was being crossed at any time, with the grid lines being readily identifiable. Estimates of home-range size were derived from the number of 5 m squares entered, or enclosed, during a 60 min period.

Behavioural observations, including the frequency of aggressive displays and chases, were used to determine whether home-ranging individuals were territorial or not. The movement results were derived from 100 h of observation over the grid and a further 100 h over the remaining reef area.

### *2.2.3 Long-term Movements:*

For the long-term study, fish traps were used to capture fish greater than 15 cm total length. The traps were rectangular, measuring 150 x 90 cm, were constructed with a framework of 6 mm dia. steel rod, and were covered by heavy cotton 1 cm mesh netting. A trap door for releasing fish was placed at one end, while the other end had a funnel of 20 cm dia. to allow fish entry. The traps were positioned on the bottom by a diver and

were baited *in situ* with crushed sea urchins (*Heliocidaris erythrogramma*). Traps were set for 1 h periods, and in daylight hours only. When the traps were pulled, captured fish were placed in a bin of seawater until they could be tagged. Fish were tagged with small T-bar tags (Hallprint), inserted at the base of the dorsal fin. All tags were printed with an individual code. Fish tagged over the grid used for the short-term movement study were tagged with T-bar tags additionally color coded with a waterproof paint to aid in underwater identification of individual fish. After tagging, fish length, apparent sex, and position on the reef were recorded before release.

Traps were positioned at random on the reef to maximise the possibility of even the most sedentary species encountering a trap during each trapping session, although the reef was arbitrarily divided into sixteen 20 m longshore x 25 m offshore sectors to simplify analysis of movement patterns. Ranges were determined on the basis of the number of sectors in which individuals were recaptured throughout the study. Because the reef had little offshore extension (20-25 m) and few fish ever crossed the sand-reef interface, the study was considered to be one dimensional with movement around the island being the movement of interest. Initial visual observations of movement indicated that a finer resolution study in two dimensions was unnecessary as movements in excess of 20 m were observed in all species.

The nearest adjacent reef, at Ninepin Point, approximately 1 km away, was searched periodically to identify any individuals migrating between reefs. Tags were printed with a return address to facilitate the return of fish captured by net fishermen who intensively gillnet reefs near Arch Rock during the summer months. The study site itself was protected for the duration of the study by a temporary government ban on net fishing.

Fish were tagged and recaptured over a 2.5 year period between May 1990 and January 1993 with weekly sampling for the first 9 months and then with month long sampling at 3-monthly intervals. The recapture results were used to estimate the net survival rate of

tagged fish; an estimate which includes loss due to emigration, mortality, and tag shedding. This estimate may be of use in assessing levels of emigration in species where rates of natural mortality and tag loss may be assumed to be small. Fish were not double tagged to estimate rates of tag shedding because of concerns of the possibility of increased tag-induced mortality. The method of Fischer and Ford (from Begon 1979) was used to estimate annual survival rates as it calculates the average survival rate over the whole recapture period, rather than for individual periods as in the stochastic methods ( e.g. Jolly/Seber, from Begon 1979). This characteristic is important in data sets with small numbers of captures and recaptures, as it minimises the effect that sampling errors have on the estimate, by combining information from all recapture periods. In the method of Fischer and Ford the estimate of population survivorship is derived by an iterative process, using a number of survivorship estimates until the observed total days survived by marks is equalled by a theoretical estimate of total days survived by marks in the population when the survivorship estimate is applied to the capture data.

The long-term recapture data for each species were analysed by  $\chi^2$  contingency tables to examine the significance of inter-specific differences in the estimated distribution of individuals amongst five range-size categories, and for any evidence of intra-specific length or sex related differences amongst these categories. The cells for the contingency tables contained the number of fish whose maximum observed range fell within each of the range categories, 0-20 m, 20-40 m, 40-60 m, 60-80 m, 80-100 m, > 100 m. Where the number in any cell fell below five, adjacent range categories were pooled. Any individuals which changed sex during the course of the study were excluded from the test of sex related differences, and likewise, individuals which grew from one size category to the other were excluded from the size related comparison. For the length related comparisons, only two size classes were compared (small : large) and the cut-off point for each class was arbitrarily chosen to ensure as even a balance of numbers between classes as possible.

## 2.3 Results

### 2.3.1 *Short-term Movements:*

Attempts to map the home-ranges of individually recognised fish failed due to rapid algal fouling of the colour-coded tags used for identification. Tags usually became fouled within 2-3 weeks, and before sufficient points could be mapped to determine home-ranges by the polygon method. Estimates of home-ranges of individual fish were therefore made by following and mapping the movement of individuals over the grid for 1 h periods. The results of these short term movement observations are summarised in Table 2.2.

2.3.1.1 *Notolabrus tetricus*: One hour movement maps were compiled for both females and males. These indicated that both males and females were active within a home-range, swimming almost continuously and covering most of the area within their range during this period. Female home-ranges were estimated to range from 225-725 m<sup>2</sup> and extended over the full depth range of the reef, usually overlapping those of many other females and two or three males. While there were frequent displays of aggression between juveniles and between females, there was no evidence of territorial defence by either group. The range of juveniles appeared to be restricted to approximately two grid sectors (50 m<sup>2</sup>) however this was not able to be verified as they were highly cryptic and were rarely able to be followed for more than 5 min before eluding the observer. Males were highly territorial and patrolled clearly defined ranges, with any intrusion by a neighbouring male resulting in a chase. The three males, whose territory overlapped the study grid, had estimated territorial ranges of 400-775 m<sup>2</sup>. During the breeding season (mid-August to January) males continuously courted the females within their territory, displaying with a raised caudal fin as they passed each female.

Table 2.2. Results of behavioural observations on six temperate reef fishes, at Arch Rock, Tasmania. Range estimates were derived from (N) individuals, each followed for 1 h.

Species	Sex	Number (N)	Estimated range	Territorial ?	Home ranging ?
<i>Notolabrus</i>	male	3	400-775 m <sup>2</sup>	yes	-
<i>tetricus</i>	female	5	225-725 m <sup>2</sup>	no	yes
<i>Notolabrus</i>	male	5	>70x25m	no	?
<i>fucicola</i>	female	5	>70x25m	no	?
<i>Pictilabrus</i>	male	1	175 m <sup>2</sup>	yes	-
<i>laticlavus</i>	female	0	?	?	?
<i>Pseudolabrus</i>	male	2	280-330 m <sup>2</sup>	yes	-
<i>psittaculus</i>	female	3	325-375 m <sup>2</sup>	no	yes
<i>Penicipelta</i>	male	5	?	no	?
<i>vittiger</i>	female	5	?	no	?
<i>Meuschenia</i>	male	5	>70x25m	no	?
<i>australis</i>	female	5	>70x25m	no	?

2.3.1.2 *Notolabrus fucicola*: All individuals, whose movements were mapped, ranged freely over the entire grid (70 m x 25 m) during a one hour period. Over the duration of the study, several distinctly marked individuals were seen on numerous occasions and on all sectors of the reef, indicating that at least some individuals had ranges equal to, or in excess of, 1 ha. While males were frequently involved in chases during the breeding season (mid-August to January), there was no evidence of territorial behaviour, with males and females occupying continuously overlapping home-ranges. Males constantly followed females during the breeding season, occasionally displaying to them with raised dorsal and anal fins, until being either chased off by another male or swapping to follow another female.

2.3.1.3 *Pictilabrus laticlavus*: The cryptic coloration of juvenile and female fish made them difficult to see, and this, combined with their habit of hiding amongst the algal canopy, prevented a detailed study of short-term movements in this species.

Observations of males in the breeding season (Late August to January) indicated that

they may be territorial as frequent chases were observed, and one male observed for 60 min actively patrolled a home-range of 175 m<sup>2</sup>, chased off all male intruders and courted females.

2.3.1.4 *Pseudolabrus psittaculus*: In this species females actively swam within overlapping home-ranges of approximately 325-375 m<sup>2</sup>, which were restricted to the deeper parts of the reef (5-10 m). Males were territorial with estimated ranges of 280-330 m<sup>2</sup>, and chased off any male intruders. During the breeding season (Late August to January) males regularly displayed to the females within their territory with a raised caudal fin.

2.3.1.5 *Penicipelta vittiger*: Although many adult fish were present over the grid, their behaviour limited meaningful observation because while feeding on their primary food source (epiphytic invertebrates), individuals hardly moved for periods in excess of 60 min, except to adjacent plants. When mobile, individuals crossing the observation grid displayed no evidence of site-attachment at this scale, or of territorial behaviour. During the breeding season (September to January) males constantly followed females until either swapping to another female or being involved in a chase with another male, with the chase usually resulting in both males losing contact with the female.

2.3.1.6 *Meuschenia australis*: Short-term movements of both sexes were on a scale larger than the grid, and there was no evidence of site-attachment at that scale. Males and females shared broadly overlapping home-ranges and there was no indication of territorial behaviour by either sex. During the breeding season (September to January) males were often seen following females for extended periods. Interactions between males were infrequently observed, possibly due to the low population density of this species.

### 2.3.2 Long-term Movements:

Over a period of 2.5 years, 1294 fish were tagged on the reef surrounding Arch Rock, and 2601 recaptures were recorded. During this time, extensive diving surveys of the adjacent reef systems at Ninepin Point failed to detect any immigrants from Arch Rock, although two *P. vittiger* were captured at nearby sites by recreational fishermen. One of these had travelled 1.5 km (to White Rock, near Ninepin Point), the other 4.5 km (to Charlotte Cove), with both movements from Arch Rock involving the crossing of extensive areas of open sandy bottom.

Annual loss rates calculated from recapture data using the method of Fischer and Ford (from Begon 1979) gave an indication of the rates of emigration for some species (Table 2.3, calculated from the capture data shown in Table 2.4), as loss is equivalent to emigration plus mortality (including tag loss).

Table 2.3. Average annual survival rate estimates for six temperate reef fishes at Arch Rock, Tasmania, calculated using the method of Fischer and Ford (from Begon 1979). Table includes summary data on the number of recapture events, the number of individual fish tagged, and the total number of recaptures over the period of the study. The raw data used to estimate survival rate is presented in table 2.4.

	<i>Notolabrus tetricus</i>	<i>Notolabrus fucicola</i>	<i>Pictilabrus laticlavius</i>	<i>Pseudolabrus psittaculus</i>	<i>Penicipelta vittiger</i>	<i>Meuschenia australis</i>
Recapture period	6/90-3/91	6/90-5/91	8/90-8/91	8/90-5/91	6/90-3/91	6/90-3/91
Recapture events	12	12	7	6	8	12
Number tagged	278	63	49	53	87	60
Number of recaptures	122	150	19	56	32	170
Estimated survival rate	1.00	1.00	0.13	0.60	0.37	1.00



Table 2.4. Recapture data used in the estimation of annual survivorship in Table 2.3.

(a) *Notolabrus tetricus* recapture data.

Recapture period	Days since 0	Captures	Recaptures	Period of first capture											
				1	2	3	4	5	6	7	8	9	10	11	
1	0	9	0												
2	26	11	0	0											
3	88	34	0	0	0										
4	95	22	0	0	0	0									
5	123	2	0	0	0	0	0								
6	145	35	12	4	0	5	3	0							
7	162	24	11	0	1	7	3	0	0						
8	172	31	13	1	0	5	1	0	5	1					
9	192	9	7	0	1	3	3	0	0	0	0				
10	203	25	31	2	1	7	4	0	10	2	4	1			
11	265	76	34	0	4	10	5	0	4	5	3	2	1		
12	279	9	14	1	1	3	0	0	1	0	4	0	4	0	

(b) *Notolabrus fucicola* recapture data.

Recapture	Days	New	Recapture	Period of first capture											
period	since 0	captures	s	1	2	3	4	5	6	7	8	9	10	11	
1	0	10	0												
2	26	10	3	3											
3	88	7	5	3	2										
4	95	11	5	2	2	0									
5	123	4	1	1	0	0	0								
6	145	8	17	5	3	2	4	3							
7	162	8	14	3	4	2	1	1	3						
8	172	0	15	2	2	2	3	2	4	0					
9	192	0	13	5	3	0	0	0	3	2	0				
10	203	2	33	7	4	5	5	4	4	3	0	0			
11	265	2	29	5	6	4	3	1	5	4	0	0	1		
12	279	1	15	3	1	5	1	0	4	1	0	0	0	0	

(c) *Pictilabrus laticlavius* recapture data.

Recapture period	Days since 0	New captures	Recaptures	Period of first capture					
				1	2	3	4	5	6
1	0	3	0						
2	60	11	3	3					
3	90	12	2	0	2				
4	120	7	5	0	3	2			
5	180	12	3	0	1	1	0		
6	210	4	2	0	1	0	1	0	
7	270	20	4	0	1	0	2	1	0

(d) *Pseudolabrus psittaculus* recapture data.

Recapture period	Days since 0	New captures	Recaptures		Period of first capture					
			1	2	3	4	5	6		
1	0	10	0							
2	57	16	1	1						
3	78	9	4	2	2					
4	112	10	13	2	7	4				
5	181	8	18	2	7	6	3			
6	261	9	20	1	9	5	4	1		

(e) *Penicipelta vittiger* recapture data.

Recapture period	Days since 0	New captures	Recapture s	1	2	Period of first capture						
						3	4	5	6	7		
1	0	17	0	0								
2	60	12	2	2								
3	120	12	3	3								
4	150	23	6	3	2	1						
5	180	6	4	0	0	2	1					
6	240	11	2	0	0	1	1					
7	270	6	2	0	0	1	1					
8	330	18	13	2	1	1	2	1	3	3		

(f) *Meuschenia australis* recapture data.

Recapture period	Days since 0	New Captures	Recapture s	Period of first capture										
				1	2	3	4	5	6	7	8	9	10	11
1	0	30	0											
2	26	6	9	9										
3	88	6	19	19	0									
4	95	0	15	12	3	0								
5	123	1	5	4	0	1	0							
6	145	2	29	21	3	5	0	0						
7	162	2	32	22	2	6	0	0	2					
8	172	1	23	17	1	4	0	0	0	1				
9	192	1	23	14	1	5	0	0	1	1	1			
10	203	2	27	20	0	5	0	0	1	1	0	0		
11	265	8	29	20	2	4	0	0	2	1	0	0	0	
12	279	1	14	12	0	1	0	0	1	0	0	0	0	0

In three species, *N. tetricus*, *N. fucicola*, and *M. australis*, annual survivorship was estimated at 100% which indicates that if any emigration occurs in these species, rates must be low. The unusually high annual survivorship estimates appear to be related to intra-specific variability in trap response, as in each of these species a number of individuals were strongly attracted to the traps and were captured during most recapture

events, thus inflating the observed total days survived beyond that expected if trapping was completely at random. *Pictilabrus psittaculus* had an estimated annual survivorship of 60%, and although mortality, tag loss and emigration cannot be separated, such a high survivorship still indicates that any emigration must be at low levels.

The survivorship estimates for *P. vittiger* (37 %) and *P. laticlavius* (13%) were considerably lower than the remaining species and cannot be used as an indication of emigration rates due to confounding by mortality and tag loss. However, these low values probably reflect high levels of natural mortality, or tag loss due to factors other than mortality, rather than high levels of emigration. *Penicipelta vittiger* is a short lived species, living between 2 to 3 years (Chapter 3) and would therefore be expected to have high levels of natural mortality, particularly as most tagged individuals in this species would have been already at least 1 year old at tagging. A large number of *Pictilabrus laticlavius* caught during the trapping period had tag scars, presumably due to tag loss caused by abrasion related to this species close affinity with the substrate, indicating a potential source of bias in annual survivorship estimates.

The long-term home-range patterns estimated from recaptures over a 2.5 year period between May 1990 and January 1993 are shown in Fig. 2.2, with summary data in Table 2.5. As all species displayed considerable intra-specific variability in home-range size, the results in Fig. 2.2 are presented as the cumulative percentage of individuals which were always recaptured within each maximum range. The majority of individual *N. tetricus*, *N. fucicola*, *P. laticlavius*, *P. psittaculus*, and *P. vittiger* had estimated home-ranges of less than 100 m x 25 m during this period, although a significant proportion of *N. fucicola* (43%) had an estimated range in excess of 100 m x 25 m. The high average days between first and last capture (Table 2.5) indicated that these patterns were stable over time and not just the result of short-term residency. *Meuschenia australis* was the most wide-ranging species with only 15% of individuals always being recaptured within a range of 100 m x 25 m or less.

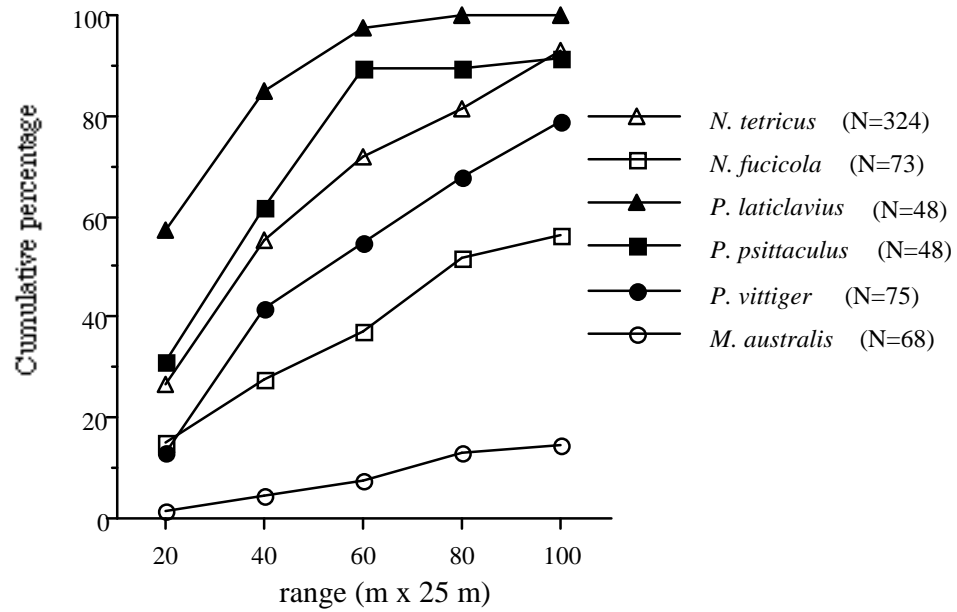


Figure 2.2. Intra-specific home-range variation identified from recaptures of tagged fish at Arch Rock, Tasmania, between May 1990 and January 1993. Calculated from the maximum observed ranges of fish recaptured at least once and plotted as the cumulative percentage of individuals always recaptured within a range equal to or less than the range shown.

Table 2.5. Summary data of the movements of six species of temperate reef fish at Arch Rock, Tasmania. Derived from a 2.5 year recapture study, between May 1990 and January 1993.

Species	Captures	Recaptures	Mean recaptures per individual	Highest recaptures per individual	Percentage recaptured at least once	Average days between first and last capture
<i>Notolabrus tetricus</i>	612	644	1.1	14	53	287
<i>Notolabrus fucicola</i>	103	588	5.7	43	71	370
<i>Pictilabrus laticlavus</i>	183	90	0.5	8	26	249
<i>Pseudolabrus psittaculus</i>	85	155	1.8	11	56	398
<i>Penicipelta vittiger</i>	214	170	0.8	22	35	178
<i>Meuschenia australis</i>	97	954	9.8	46	70	402

Using the values from Fig 2.2, a pairwise comparison by  $\chi^2$  of the difference between the range-size of each species showed all species to be significantly different from each other, at least at the 0.05 significance level (Table 2.6). The range-size order by species was *P. laticlavius* < *P. psittaculus* < *N. tetricus* < *P. vittiger* < *N. fucicola* < *M. australis*, with the three territorial species having smaller estimated ranges than those of the other species.

Table 2.6. Results of pairwise comparisons by  $\chi^2$ , using contingency tables based on long-term recapture results (from Fig. 2.2), of the distribution amongst 5 range size categories of six temperate reef fishes ( $H_0$ : range of species 1 = species 2). Results are given as probability and (degrees of freedom).

Species	<i>Notolabrus tetricus</i>	<i>Notolabrus fucicola</i>	<i>Pictilabrus laticlavius</i>	<i>Pseudolabrus psittaculus</i>	<i>Penicipelta vittiger</i>
<i>Notolabrus fucicola</i>	0.0001(5)				
<i>Pictilabrus laticlavius</i>	0.0001(5)	0.0001(3)			
<i>Pseudolabrus psittaculus</i>	0.0462(3)	0.0001(3)	0.0252(3)		
<i>Penicipelta vittiger</i>	0.0015(5)	0.0253(4)	0.0001(3)	0.0003(3)	
<i>Meuschenia australis</i>	0.0001(2)	0.0001(2)	0.0001(2)	0.0001(2)	0.0001(2)

When the long-term recapture results for each species were examined by a  $\chi^2$  test for sex-related differences in home-range size, none were detected (Table 2.7). The results were then examined by a  $\chi^2$  test for length related differences in home-range size (Table 2.8). In four species, *N. tetricus*, *P. laticlavius*, *P. psittaculus* and *M. australis*, length was significantly related to range size, with ranges increasing with length.

The labrid species are almost certainly permanent residents of the study reef as no emmigrants were detected during extensive surveys of adjacent reefs, and no tags were returned from local fishermen. This observation is in addition to the low estimated mortality rates for *N. tetricus*, *N. fucicola*, and *P. psittaculus*, which indicate that any

loss due to emigration must be low (Table 2.3), as well as the high average days between first and last capture for all of these species (Table 2.5).

Table 2.7. Results of  $\chi^2$  tests, based on contingency tables derived from the long-term recapture results, of the influence of sex on the distribution amongst 5 range size categories of six temperate reef fishes ( $H_0$ : range of males = females).

Species	Females	(N) Males	Degrees of freedom	Significance level (p)	Significant result (Y:N)
<i>Notolabrus tetricus</i>	301	23	2	0.92	N
<i>Notolabrus fucicola</i>	47	19	1	0.16	N
<i>Pictilabrus laticlavus</i>	15	33	1	0.87	N
<i>Pseudolabrus psittaculus</i>	41	7	1	0.98	N
<i>Penicipelta vittiger</i>	35	26	2	0.82	N
<i>Meuschenia australis</i>	38	30	1	0.46	N

Table 2.8. Results of  $\chi^2$  tests, based on contingency tables derived from the long-term recapture results, of the influence of fish length on the distribution amongst 5 range size categories of six temperate reef fishes ( $H_0$ : range of small = large,  $H_1$ : range of small < large).

Species	(N) Small Large		Length classes compared (cm)	Degrees of freedom	Significance level (p)	Significant result (Y:N)
<i>Notolabrus tetricus</i>	51	206	15-20 : 20+	2	0.044	Y
<i>Notolabrus fucicola</i>	19	55	15-25 : 25+	1	0.521	N
<i>Pictilabrus laticlavus</i>	25	22	15-21 : 21+	1	0.014	Y
<i>Pseudolabrus psittaculus</i>	31	14	15-20 : 20+	1	0.018	Y
<i>Penicipelta vittiger</i>	20	41	19-25 : 25+	2	0.892	N
<i>Meuschenia australis</i>	18	49	15-21 : 21+	1	.001	Y

While short term visual observations on the monacanthid species *P. vittiger* and *M. australis* failed to identify any clear patterns of spatial utilisation, the long-term recapture data provides some indications. *Penicipelta vittiger* displayed the strongest tendency for site-attachment with 79% of recaptured individuals always being recaptured within a range of 100 m x 25 m or less. With a moderate recapture rate (35% recaptured at least once) and a high average days between first and last capture (178 days), it appears likely that the majority of individuals are permanent residents of the reef. Recapture rates and days between first and last capture may be lower than those estimated for the labrid species and *M. australis* as a result of the comparatively short lifespan of *P. vittiger* (Chapter 3). While two tag returns from local fishermen indicate that this species can move considerable distances (1.5 and 4.5 km) and across major habitat boundaries, it appears that these individuals represent only a small percentage of the population. Extensive searches of adjacent reefs found no evidence of immigrant *P. vittiger*, which would have been expected if emigration rates were higher.

For *M. australis*, the long-term recapture data indicated that only a small proportion of individuals were always recaptured within a range of 100 m x 25 m or less (Fig. 2.2). While a study over larger spatial scales is needed to determine whether or not the majority of individuals are home-ranging, the results of the present study suggest that most individuals were at least permanent residents of the reef. This is indicated by the high average days between first and last capture (402 days), the very high proportion recaptured at least once (70%), and the annual survivorship estimate of 100 %.

## **2.4 Discussion**

The short and long-term movement patterns of the labrid species observed during this study appear similar to those described for other temperate labrids such as *Pseudolabrus celidotus*, reported by Jones (1984) and fall within the range of behaviours described for labrids in general (Thresher 1984). *Notolabrus tetricus*, *Pictilabrus laticlavius* and

*Pseudolabrus psittaculus* are site-attached protogynous hermaphrodites, where females have widely overlapping home-ranges and males are territorial, at least during the breeding season, and exclude all other males from their range. *Notolabrus fucicola* is unusual in that it is not hermaphroditic, although a similar sexual system has now been described in three northern European labrids (Costello 1991) and this sexual system may be more common than previously thought, at least in temperate regions. However, unlike the northern European labrids where males are territorial (Costello 1991), the social system of *N. fucicola* is more similar to that of the Caribbean species *Halichoeres garnoti* described by Thresher (1979), where spawning is promiscuous and home-ranges are broadly overlapping.

Behavioural observations indicated that neither monacanthid species displayed evidence of territorial behaviour, and many individuals had overlapping ranges. This contrasts with the territorial behaviour reported by Barlow (1987) for large individuals of a tropical monacanthid species, the longnose filefish *Oxymonacanthus longirostris* and for several species in the related family Balistidae, including the tropical species *Odonus niger* and *Pseudobalistes fuscus* (Fricke 1980) and *Sufflamen verres* (Thresher 1984). As the monacanthids are predominantly a temperate and sub-tropical family (Randall *et al.* 1990), and observation-based temperate research is generally limited by cold and low visibility water, there are few published descriptions of their behaviour, and more studies are needed before a general understanding of their typical movement patterns emerges.

The long-term movement results indicated that there was considerable intra-specific variation in range size, and while this was not found to be sex-related in any of the species examined, range size was found to increase in proportion to the size of individuals in four of the six species examined. This size related relationship has been described in tropical species (Sale 1978) for at least one other temperate species (Jones



1984) and is a relationship that may apply in many resident species on both temperate and tropical reefs.

Regardless of sexual systems and behaviour, all six species appeared to be permanent residents of the reef and, in this, the results of this study on common southern hemisphere temperate reef fishes are in keeping with those of Davis and Anderson (1989) on common northern hemisphere temperate reef fishes. Permanent residency may be a characteristic of many temperate reef species, and is a feature previously described for tropical reef fishes (Ehrlich 1975). This result is not unexpected as familiarity with a section of reef offers many advantages such as an intimate knowledge of feeding, sleeping and shelter sites, and these advantages should not be expected to vary between tropical and temperate reefs.

Unlike some temperate regions where environmental extremes force offshore movements (Parker 1990) or hiding and torpor (Olla *et al.* 1979), all species under investigation remained present and active throughout the year, probably because of the small seasonal water temperature variation of 8-18°C at this site compared to that described by Parker (1990) for North Carolina (6-28°C). As large seasonal water temperature variations have not been reported for southern Australia, it is likely that the results from this study can be extended to other sites and species, suggesting a general trend for year-round residency in the southern Australian reef fish fauna.

The natural habitat boundary of 1 km of open sandy bottom between the study site and the nearest adjacent reef system appeared to severely restrict the movement of post-recruitment reef fish. There was no evidence of movement across this boundary by the labrids and only limited evidence of emigration of monacanthid residents, even though some individuals of *N. fucicola* and *Meuschenia australis* were known to range over the entire reef on a daily basis. The 4.5 km movement recorded for one *P. vittiger* does indicate that movements across boundaries and over long distances are possible but this

is likely to be restricted to a small percentage of the population, and similar intra-specific variability in behaviour has been recorded in several tropical species (Bohnsack 1990).

The effectiveness of natural habitat boundaries in preventing emigration, and the long and short-term scales of movement in resident fishes, should be important considerations in the future design and management of marine reserves on temperate reefs where protection of local fish populations is desired. This is especially the case for small reserves such as the Ninepin Point and Bicheno reserves in Tasmania where the core protected area consists of only 1 km of coastline. Species such as *N. fucicola*, and *Meuschenia australis* are capable of daily movements of at least 180 m in one dimension, and movements of 230 m in just 10 minutes have been reported by Leum and Choat (1980) for *Cheilodactylus spectabilis*, another common temperate reef resident. These movements imply that a significant proportion of some species may range outside of a small (1 km) reserve as part of their normal daily behaviour and be subject to fishing mortality. To address this problem, the minimum reserve diameter should be at least an order of magnitude greater than the daily movements of the most wide-ranging residents in order to minimize losses. Where the creation of appropriate sized reserves is not possible, sites should be selected where natural habitat boundaries can be used to isolate the reserve from adjacent areas, effectively fencing in the protected population.

## Chapter 3 Growth

### 3.1 Introduction

To allow for comparisons of inter-population variability in growth rates (discussed in Chapter 6) it was first necessary to establish and validate a reliable method of ageing each of the species in this study. Of the six species under investigation, only the growth of *N. tetricus* has been previously reported (Shepherd 1985). As that study was in South Australia where growth rates may differ from south eastern Tasmania, it was considered necessary to further investigate growth in this species.

The two most conventional methods of ageing temperate fishes are the counting of assumed annual growth rings on scales and otoliths (Jearld 1983). Growth rings in the otoliths of temperate fishes have been shown to be directly related to seasonal changes in water temperature which causes resulting changes in the metabolic and growth rates of fish (Williams and Bedford 1974). Otoliths consist of calcium carbonate crystals deposited in an organic matrix (Degens *et al.* 1969). Changes in temperature result in changes in the ratio of calcium carbonate to organic protein, producing alternating translucent and opaque zones when viewed by light microscopy. The growth of scales in many temperate species is periodical with relatively short periods of growth usually followed by longer periods of slow or no growth (Beamish and McFarlane 1987). These changes in growth are reflected in the density of circuli on the scales which can be used for ageing.

While in the past, the reading of scales has been accepted as a routine and accurate method of ageing, with little or no effort towards validation (Beamish and McFarlane 1987), recent reviews of scale and otolith ageing literature where validation has been attempted, indicate that counts of scale, and even otolith surface annuli, can sometimes under estimate the true age of fish greater than 10-20 years by a factor of up to 3x (Beamish and Chilton 1981, Beamish and McFarlane 1987). This is particularly the

case in species with an asymptotic growth curve. Such findings highlight the need for effective validation of the chosen techniques.

The most reliable means of validation appears to be mark-recapture studies (Hales 1989), in particular ones where hard parts are time marked with oxytetracycline or another label able to be identified in subsequent hard part analysis. This method was used effectively by Francis *et al.* (1992) to validate the use of otolith annual ring counts of adult snapper (*Pagrus auratus*).

In this study the length based growth was determined for the six species under investigation by a capture-recapture study at Arch Rock, Tasmania. This growth was used to validate the ages estimated from growth rings in otoliths and scales of fish collected in the immediate vicinity of Arch Rock. Validation was assisted, where possible, by diver based visual observations of the year class size structure of each species at Arch Rock.

## **3.2 Materials and Methods**

### *3.2.1 Tag-based growth estimates*

*3.2.1.1 Site and sampling details:* In order to estimate rates of growth, the six species under investigation were captured, tagged, released and subsequently recaptured at Arch Rock in the D'Entrecasteaux Channel (Fig. 2.1, Chapter 2) at regular intervals between September 1990 and January 1994. This study was conducted in parallel with a study on movement (Chapter 2) and the methods used to capture, tag and recapture fish are described in detail in that chapter. Tagging was generally restricted to fishes greater than 15 cm in total length to minimise the potential impact that tags might have on growth and mortality.

*3.2.1.2 Analysis of growth:* To simplify the analysis of growth information from recapture tagged fish, only length increments from fish at large for 10-14 months were

used. These measured increments were then adjusted pro-rata to estimates of 12 month growth. Length increments from fish recaptured during shorter and longer periods were not used due to the increased contribution of measurement errors in short-term recapture based estimates, and the likely effect of seasonal variation in growth on pro-rata estimates of annual length increment.

The length based growth relationship for each species are plotted as Ford-Walford plots with the pro-rata estimate of length at one year after tagging plotted against length at tagging. The growth data are also plotted as Manzer-Taylor plots where annual length increment is plotted against length at tagging. The von Bertalanffy parameters  $L_{\infty}$  (length at age  $\infty$ ) and K (growth constant) were estimated from this recapture data using a re-arranged and re-paramaterised version of the von Bertalanffy growth function. The version used was  $\Delta L = (L_{\infty} - L_t)(1 - e^{-K\Delta t})$  (Fabens 1965). The values of K and  $L_{\infty}$  were estimated by a least squares iterative approach using the non-linear model function of the computer statistical package SYSTAT. These parameters were estimated for comparison with those predicted from the age-length relationship determined from otolith based age estimates, to help assess the validity of assumed annual increments in otolith marks.

The Manzer-Taylor plot was used to check the von Bertalanffy estimates derived from the model, as the x intercept of the linear regression fitted to this plot is equal to  $L_{\infty}$  and the slope is equal to  $-(1 - e^{-K\Delta t})$  (Ricker 1975).

### 3.2.2 Otolith and scale based growth estimates

3.2.2.1 *Sites and collection methods*: Fish were sampled at several sites to obtain otoliths for ageing. In an initial collection of *Notolabrus tetricus* and *N. fucicola* made at Ninepin Point in September 1990, scales as well as otoliths were collected for ageing. However, a subsequent examination of these scales indicated that major growth checks were far too numerous and irregular in spacing to be annual, and would therefore be

unsuitable for ageing. For this reason only otoliths were collected for ageing in subsequent collections.

In March and April 1993 fish were sampled from four reefs in the southern end of the D'Entrecasteaux Channel adjacent to, and including, Arch Rock. These sites were at Charlotte Cove, Butts Reef, and Roaring Beach (Fig. 2.1). Only a few specimens of *Pictilabrus laticlavius* and *Pseudolabrus psittaculus* were collected in this sample, and therefore further collections were made at several sites on the Tasmanian East Coast in February 1994 to obtain sufficient specimens to examine growth in these species. The east coast sites surveyed were Fortescue Bay, Garden Point and Stinking Bay (in Port Arthur), Marion Bay, and Spring Beach (Fig 6.1).

Fish were captured using fine mesh nets with several mesh sizes (5, 7, 9, and 11 cm), as well as in traps and by spear. The trap construction is described in Chapter 2. This mixture of capture methods was used in order to sample as wide a size range as possible in each species.

After capture, fish were kept in iced seawater until they were able to be processed. During processing they were measured to the nearest millimetre in total length, and the otoliths were removed. Total length here is defined to be from the tip of the snout to the posterior most tip of the caudal fin. Otoliths were air dried for a week and then stored in glycerol for at least one day before being aged. For ageing, the otoliths of all six species were viewed whole as growth checks appeared sufficiently distinct to use this method. Thin sections of otoliths were not used as growth (for the labrids) was not consistently in one plane, especially in older individuals (7+ and older). September 1 was taken to be the nominal birth date for all species examined as this date is close to the beginning of their spawning season (Chapter 4).

3.2.2.2 *Analysis*: For each species the von Bertalanffy growth parameters  $L_{\infty}$  and  $K$  were estimated from the otolith based length at age data, using the equation  $L = L_{\infty}(1 - e^{-K(\text{Age} - t_0)})$ , where  $T_0$  = the time at which the fish would have had zero length if it had always grown in the manner described by the equation. Estimation of parameters was by least squares estimation using the non-linear model function of the computer statistical program SYSTAT. From these values the von Bertalanffy growth curve for each species was derived and plotted along with the raw data.

For the three species shown to be gonochorists in Chapter 4 (*Notolabrus fucicola*, *Penicipelta vittiger* and *Meuschenia australis*) the influence of sex on growth rate was tested using the otolith age data from the results of the Huon region survey (for *N. fucicola*) and the East Coast survey (for *P. vittiger* and *M. australis*). The data was tested by ANCOVA, examining differences in elevation and slope. Where the slope term (Sex\*Age interaction) was not significant, and with  $P > 0.25$ , the ANCOVA was repeated deleting the interaction from the model to increase the power of detecting differences in elevation. The analysis was restricted to early age classes where growth was expected to remain sufficiently linear. Residuals plots were examined to detect any age classes adding excessive shape, and to remove them from the analysis.

### 3.2.3 *Validation*

For the Ford-Walford plots, a line of best fit to the data points was fitted for each species. These were either linear relationships or polynomial, depending on the type of growth shown by each species. From these fitted models, a series of estimated lengths at age were derived, starting with the mean length at age of an early age class determined from the otolith aged fish. The minimum starting length at age was chosen to be in the range for which recapture data was available, as the growth models were not expected to adequately describe growth outside of this range. The length at age relationship derived from the Ford-Walford plot was then compared with the one determined from

otolith-based age estimates of collected fish, to assess the validity and reliability of this method of ageing.

As well as comparison with otolith-based growth curves based on the assumption of one increment per year, comparison was also made with curves based on the assumption of two increments per year, and one every two years, to determine which assumption most adequately described the observed growth. In each case, the starting point for the derivation of the length at age relationship from the tag-based growth model was assumed to be of the age predicted from the assumption being tested. This method requires no a-priori assumptions to be made regarding the real initial length at age from which the tag-based growth curves were derived. The most valid otolith based curve should simply be the one which most closely parallels the curve derived from tag-based growth.

Validation was also assisted by examining fish collections for any evidence of distinct cohorts based on size distribution, and by observing the length distributions of juvenile fishes while diving to collect fish.

### 3.3 Results

#### 3.3.1 *Notolabrus tetricus*

3.3.1.1 *Tag based growth estimates:* *Notolabrus tetricus* was the most abundant of the six species included in this study at Arch Rock between 1990 and 1994, and consequently had the most recaptures, with 196 of these being useful for estimating annual growth rates. A Ford-Walford plot showing the estimated length one year after tagging against length at tagging of fish ranging from 13-39 cm in total length is shown in Fig. 3.1A. For this plot, a linear regression best explained the relationship between length one year after tagging and at tagging over this size range, with  $y = 0.928x + 4.373$  ( $r^2 = 0.97$ ). There was no evidence of any breakpoint in this relationship which may have been evident if growth rates changed suddenly following sex-inversion.



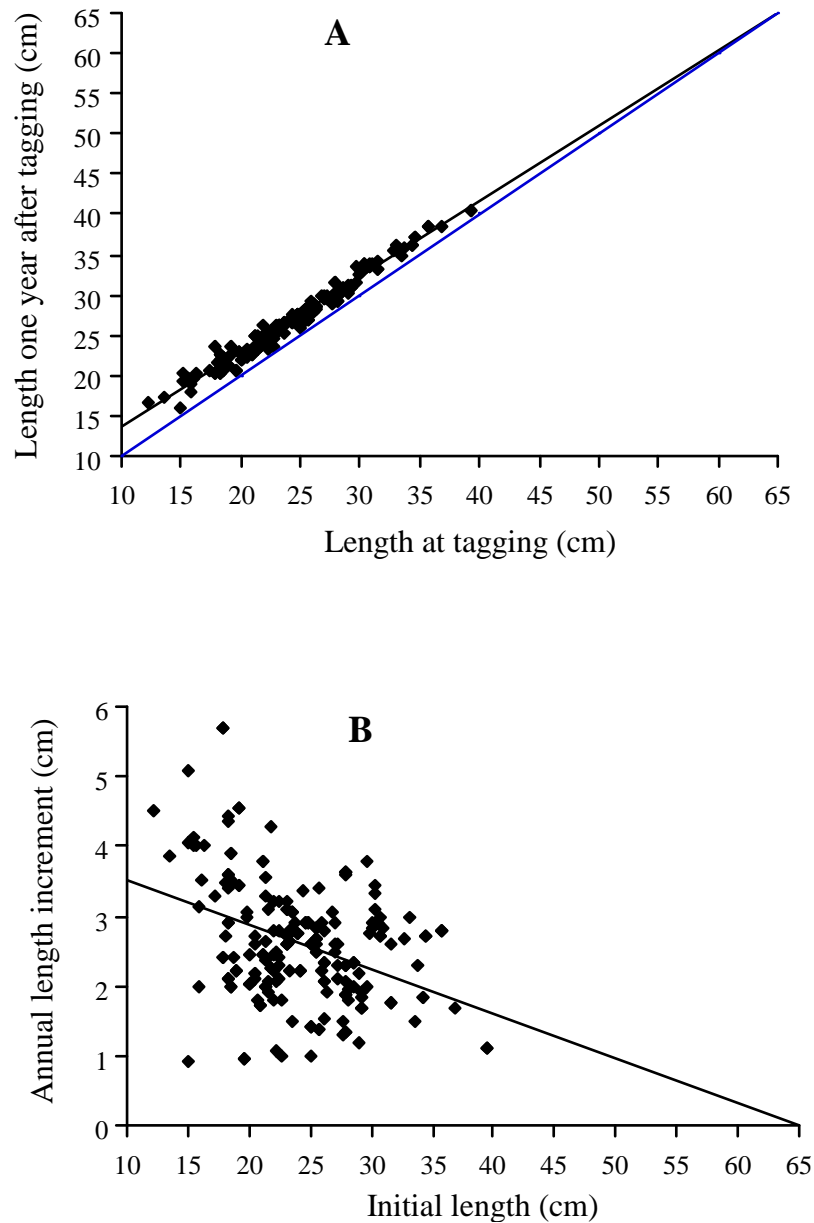


Figure 3.1 Annual growth data from 198 *Notolabrus tetricus* tagged and recaptured at Arch Rock, Tasmania, between May 1990 and January 1994. Presented as (A), a Ford-Walford plot of length at tagging against length one year after tagging, and as (B), a Manzer-Taylor plot of annual length increment against tagged length.

As well as individuals recaptured over a one year period, there were also many individuals recaptured over longer periods. While data from these longer-term recaptures could not be easily incorporated into the growth model because of the effect of seasonal growth on pro-rata estimation of annual growth, it still provides useful

information on growth. Some of this information is presented as Fig. 3.2 which shows the long-term growth curves of a selection of individuals chosen over the size range tagged.

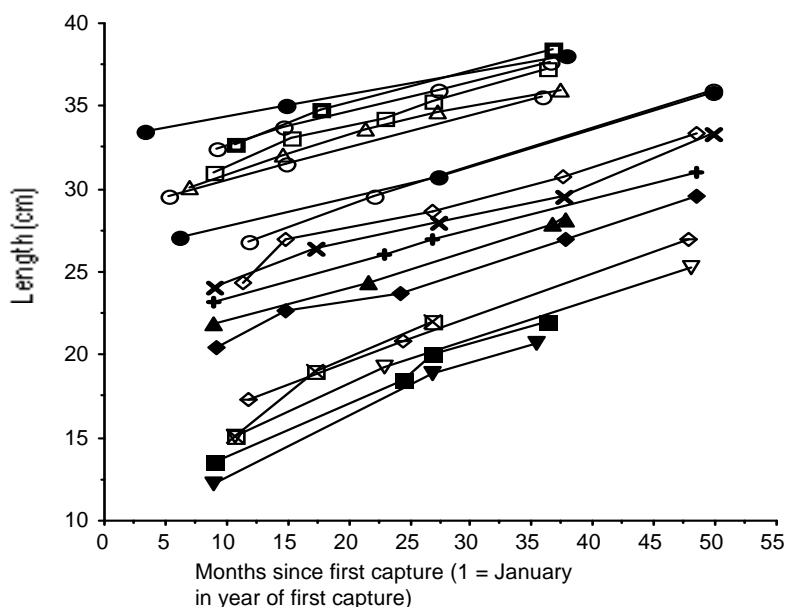


Figure 3.2 Growth trajectories of a selection of *Notolabrus tetricus* individuals representing the size range tagged at Arch Rock. Trajectories are based on recaptures between August 1990 and January 1994.

Table 3.1 Mean (s.e.) of von Bertalanffy growth parameters calculated from annual growth increments measured from tagged and recaptured fish, at Arch Rock, Tasmania, between May 1990 and January 1994.

Species	N	$L_{\infty}$ (cm)	K
<i>Notolabrus tetricus</i>	196	65.1 (6.4)	0.066 (0.010)
<i>Notolabrus fucicola</i>	82	46.3 (3.3)	0.089 (0.015)
<i>Pictilabrus laticlavius</i>	15	24.8 (0.6)	0.33 (0.06)
<i>Pseudolabrus psittaculus</i>	43	33.0 (9.8)	0.090 (0.059)
<i>Meuschenia australis</i> (Male)	29	33.8 (0.5)	0.61 (0.05)
<i>Meuschenia australis</i> (Female)	43	27.3 (0.3)	0.70 (0.06)

The von Bertalanffy growth parameters  $L_{\infty}$  and  $K$  were estimated from the growth increment data by least squares iteration (Table 3.1) giving  $L_{\infty} = 65$  cm and  $K = 0.066$ , values identical to those predicted from the Manzer-Taylor plot (Fig 3.1B).

Figure 3.1B also shows that annual growth rates can be highly variable within this species, although it appears that the variance decreases with increasing length, presumably due to factors such as the overall decrease in growth rate with age.

*3.3.1.2 Otolith based growth estimates:* To estimate the length at age relationship for *Notolabrus tetricus*, 160 fish were collected over as wide a size range as possible in the Huon region in April 1993. Ages were determined from what appeared to be annual growth rings laid down in sagittal otoliths. The annuli were usually clearly defined and both sagittal otoliths were examined to minimise reading errors. The most notable feature of the otolith annular increments was the variability in otolith radius to the first growth ring. This is probably explained by the extended spawning season of this species, as recruits spawned in late August will have a much larger period of growth until the first ring than recruits spawned in late December.

From the otolith aged fish the von Bertalanffy growth parameters were estimated (Table 3.2) and the von Bertalanffy growth curve was fitted to the length-age relationship (Fig. 3.3,  $r^2 = 0.90$ ) using these estimates. Much of the variance about this line can probably be related to differences in timing of recruitment, as well as the accumulation of differences due to differing individual growth rates. The value estimated by this method for  $L_{\infty}$  (36 cm) differed substantially from that estimated from the tagging data (65 cm).

It was not necessary to consider the influence of sex on growth in this species as it was found to be a protogynous hermaphrodite (Chapter 4) with all males being secondarily derived from mature females, and with male growth being simply a continuation of

female growth. The maximum age recorded for this species from otolith ageing was 10.5 years, in a fish collected in the East Coast collection(Fig. 6.2).

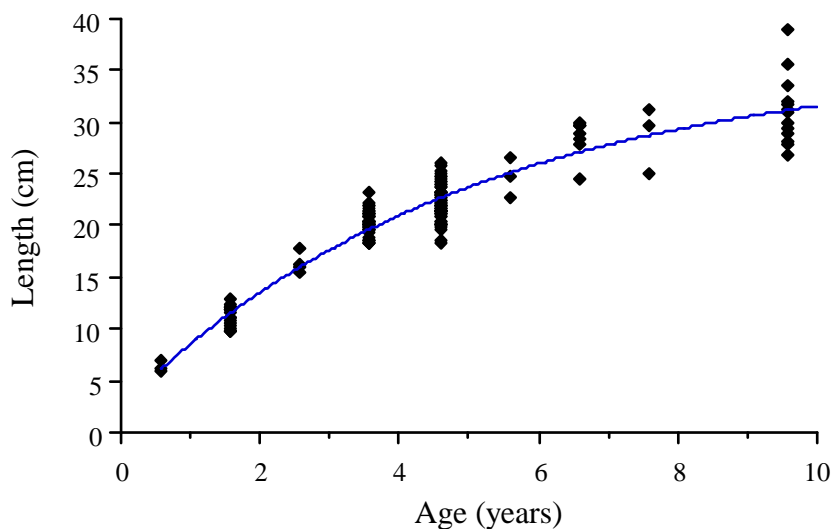


Figure 3.3 *Notolabrus tetricus* length at age relationship, for fish collected in the Huon survey (April 1993) and aged from counts of otolith annuli. The von Bertalanffy growth curve calculated from this data is fitted. Age is based on the assumption of a September 1 birthdate.

Table 3.2 Mean (s.e.) von Bertalanffy growth paramaters calculated from length at age relationships determined from fish collected in the Huon region near Arch Rock in April 1993, and aged by counting otolith annuli.

Species	N	$L_{\infty}$ (cm)	K	$T_0$
<i>Notolabrus tetricus</i>	155	36.12 (0.54)	0.20 (0.01)	-0.35 (0.06)
<i>Notolabrus fucicola</i>	58	39.90 (1.05)	0.12 (0.01)	2.36 (0.12)
<i>Pictilabrus laticlavius</i>	49	24.67 (0.25)	0.45 (0.03)	0.57 (0.13)
<i>Pseudolabrus psittaculus</i>	20	22.52 (3.81)	0.31 (0.19)	-0.66 (0.78)
<i>Penicipelta vittiger</i> (females)	29	27.36 (0.31)	1.47 (0.21)	0.82 (0.10)
<i>Meuschenia australis</i> (males)	13	37.61 (5.98)	0.32 (0.15)	0.58 (0.56)
<i>Meuschenia australis</i> (females)	19	29.14 (3.64)	0.31 (0.22)	-1.19 (1.68)

3.3.1.3 *Validation*: The validity of the first growth check is almost certain, as the 0+ and 1+ age groups were readily identifiable as distinct cohorts in their length distribution (Fig 3.3), and no individuals intermediate in size between these cohorts

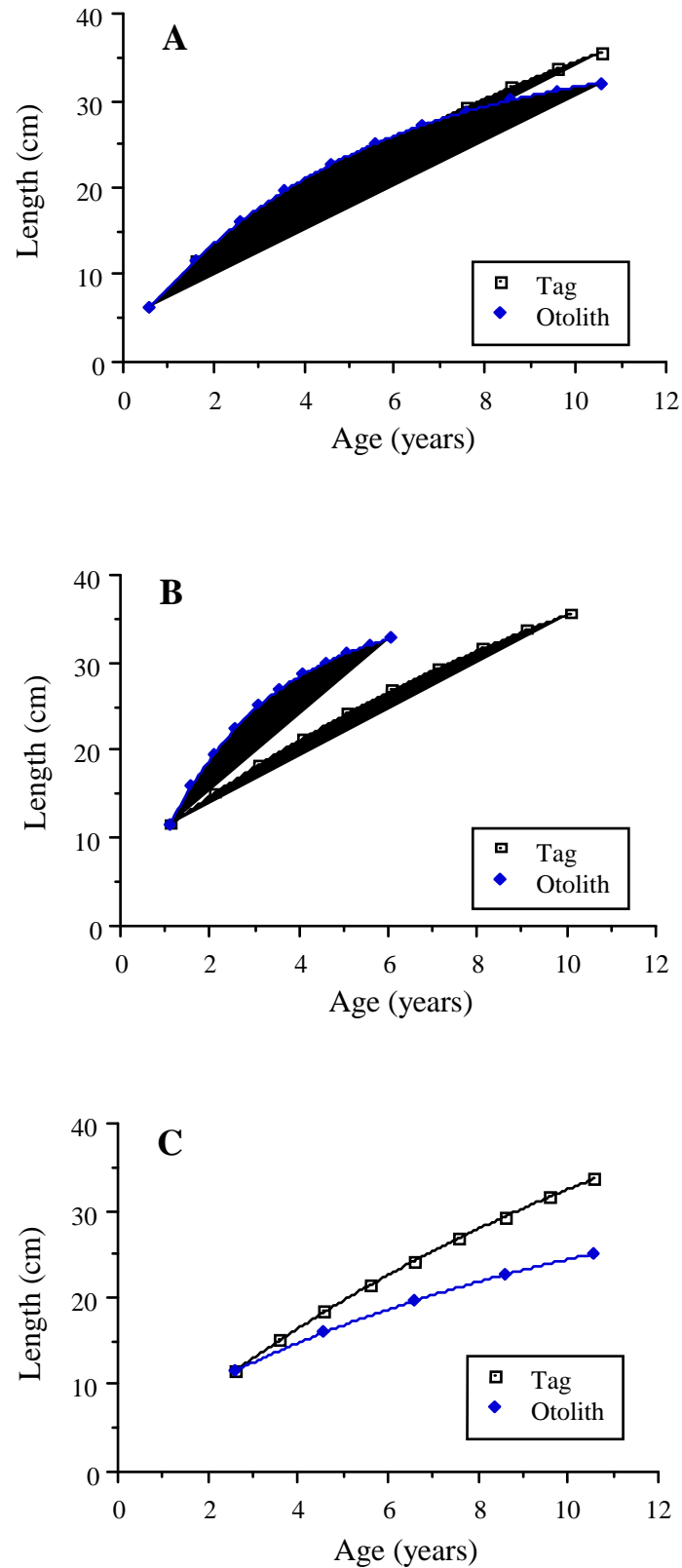


Figure 3.4 *Notolabrus tetricus*-comparison of the growth curve derived from tagged fish at Arch Rock, with the von Bertalanffy curves derived from fish collected in the Huon region (April 1993) and aged from otolith annuli under three assumptions, (A) annuli are annual, (B) produced twice yearly, (C) produced once every two years.

were observed while diving to make the collections. Likewise, the 1+ cohort was usually quite distinct from the 2+ cohort with no obvious overlap in size between the two cohorts in the fish collected (Fig 3.3).

To assess the validity of the age-length relationship based on two and more growth rings, the mean length at age of the 1+ cohort (from Fig. 3.3) was used to predict the mean lengths of ages 2+ onwards from the length based growth relationship of Fig 3.1A. The resulting growth curve was compared with von Bertalanffy growth curves obtained from otolith ageing, assuming annuli are produced annually, twice per year and once every 2 years (Fig. 3.4). There is concordance with the curve which assumed one annuli per year, indicating that otolith annuli are annual and a valid method of aging this species.

### 3.3.2 *Notolabrus fucicola*

3.3.2.1 *Tag based growth estimates:* *Notolabrus fucicola* was less abundant than *N. tetricus* at Arch Rock, and as a consequence, only 103 fish were tagged, resulting in a total of 51 recaptures being useful for deriving annual growth rate estimates. All recaptured fish were larger than 18 cm in total length at the time of tagging. A Ford-Walford plot derived from the recapture data for fish between 18 to 38 cm is shown in Fig. 3.5A. The line of best fit for this plot can be described by the linear equation  $y = 0.9149x + 3.945$  ( $r^2=0.99$ ). It was not possible to determine the extent of the influence of sex on growth from this data, because of the difficulty of reliably determining the sex of tagged fish.

Numerous individuals were recaptured over a long time frame, with times at large of up to 40 months. A selection of the growth trajectories of tagged individuals chosen to include examples from the entire size range investigated are given in Fig 3.6.

Comparison of the slopes of adjacent growth curves indicates that growth rates may vary considerably between individuals. This variability is highlighted by the Manzer-Taylor plot in Fig. 3.5B, with estimated annual length increments ranging from 1.0 - 3.5 cm in fish initially tagged at 22 cm total length.

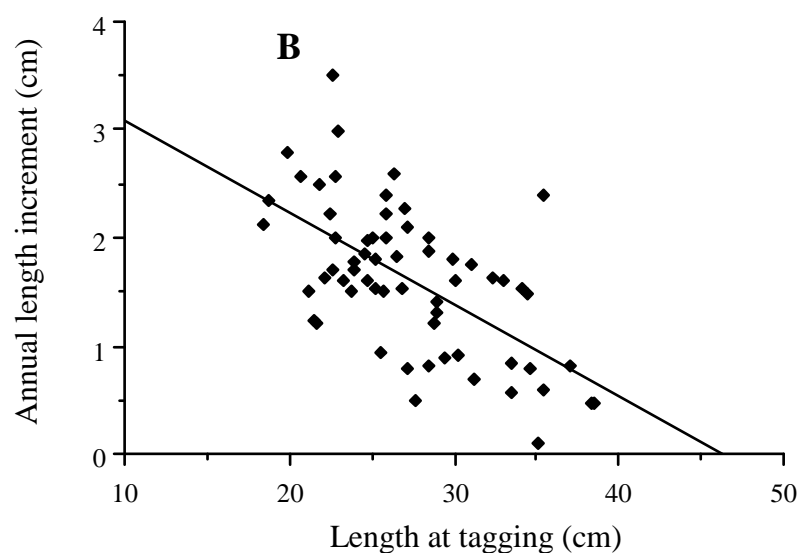
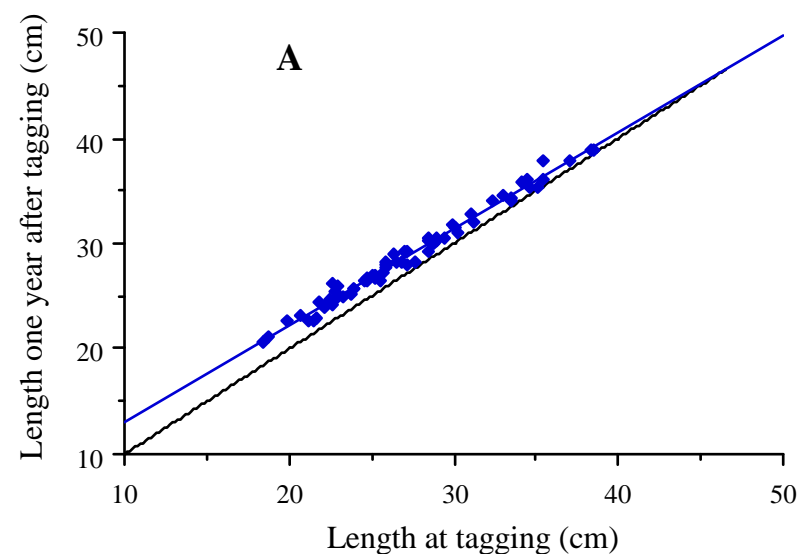


Figure 3.5 Annual growth data from 51 *Notolabrus fucicola* tagged and recaptured at Arch Rock, Tasmania, between May 1990 and January 1994. Presented as (A), a Ford-Walford plot of length at tagging against length one year after tagging, and as (B), a Manzer-Taylor plot of annual length increment against tagged length.

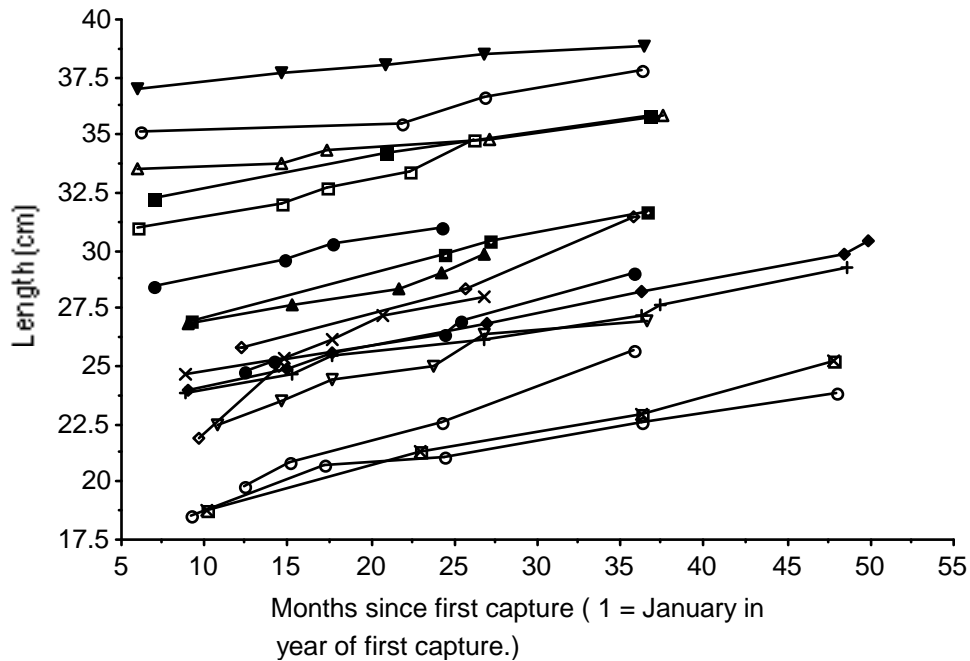


Figure 3.6 Growth trajectories of a selection of *Notolabrus fucicola* individuals representing the size range tagged at Arch Rock. Trajectories are based on recaptures between August 1990 and January 1994.

The von Bertalanffy growth parameters  $L_{\infty}$  and  $K$  were estimated from the annual length increment data by a least squares iteration (Table 3.1), giving  $L_{\infty} = 46.4$ , and  $K = .0089$ , values identical to that estimated from the Manzer-Taylor plot (Fig. 3.5B).

**3.3.2.2 Otolith based growth estimates:** To estimate the length at age relationship for *Notolabrus fucicola*, 64 fish were collected over as wide a size range as possible in the Huon region survey in April 1993. Ages were determined from what appeared to be annual growth rings in sagittal otoliths. The radius to the first growth ring varied considerably between individuals, probably due to differences in the timing of recruitment over the spring-summer period as observations of this species at Arch Rock



detected mating behaviour between late August and mid January (Chapter 4). There would therefore be at least 4 months of extra growth available to the earliest spawned individuals than to the latest spawned.

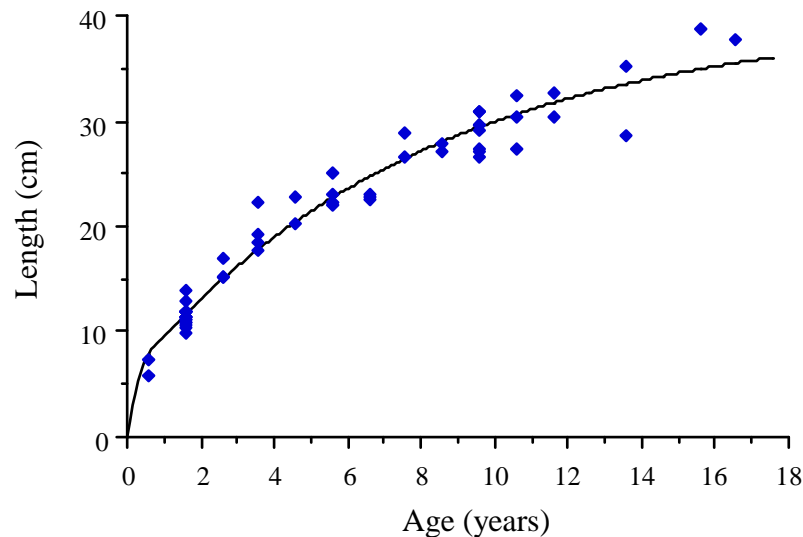


Figure 3.7 *Notolabrus fucicola* length at age relationship, for fish collected in the Huon survey (April 1993) and aged from counts of otolith annuli. The von Bertalanffy growth curve calculated from this data is fitted. Age is based on the assumption of a September 1 birthdate.

The otolith based von Bertalanffy growth parameters  $L_{\infty}$  and  $K$  (Table 3.2) were estimated from the length at age data by the non-linear model function of SYSTAT, and the von Bertalanffy growth curve derived from these estimates was fitted to the length-age plot of the raw data (Fig. 3.7,  $r^2 = 0.96$ ). This curve fitted the data and adequately describes the growth relationship, at least over the age classes collected (7 months to 17 years). Seventeen years appears to be close to the maximum age of this species as no older individuals were collected from the Huon sites in this study, or from the East Coast sites examined in Chapter 6. The estimate of  $L_{\infty}$  (40 cm) is substantially smaller than that estimated from tagging data (46 cm).

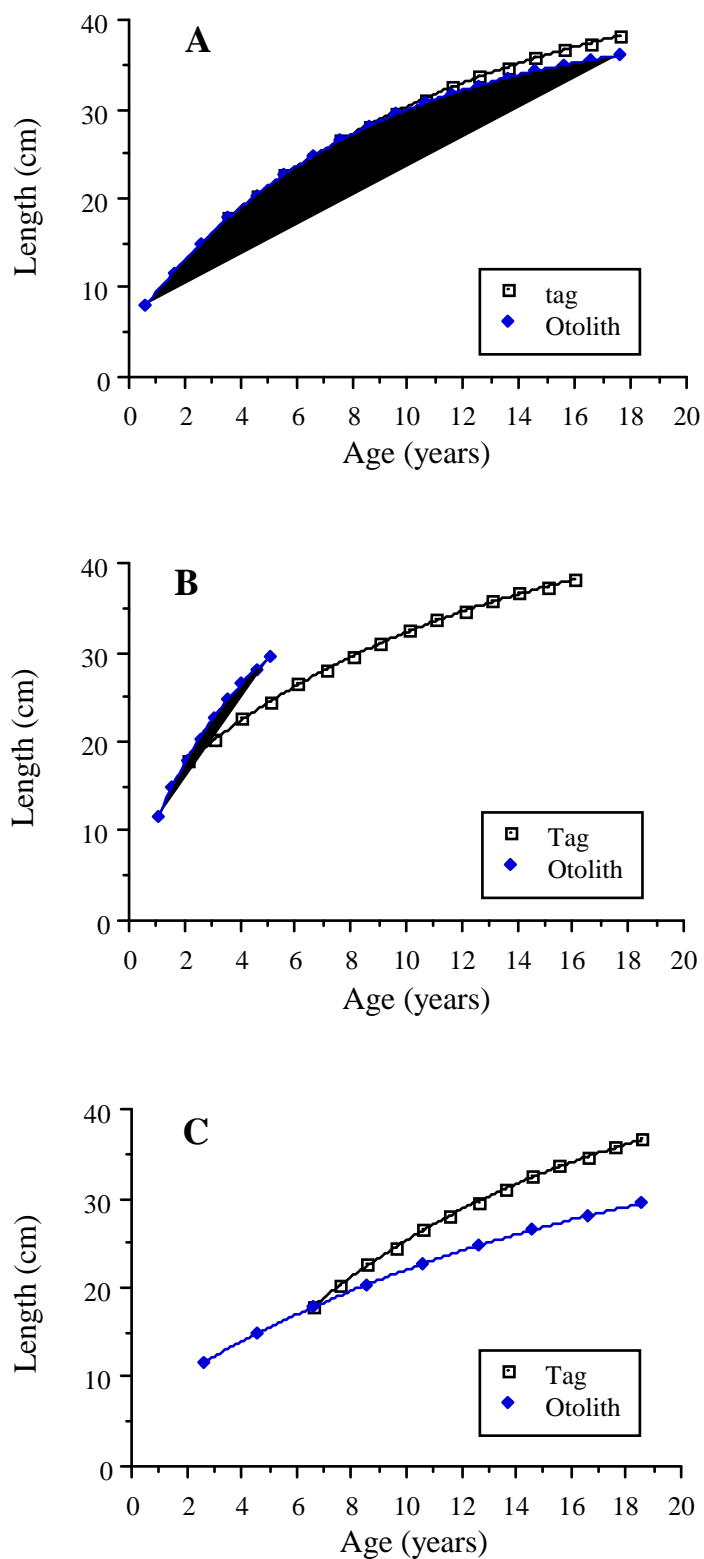


Figure 3.8 Comparison of *Notolabrus fucicola* growth curve derived from tagged fish at Arch Rock, with the von Bertalanffy curves derived from fish collected in the Huon region (April 1993) and aged from otolith annuli under three different assumptions, (A) annuli are annual, (B) produced twice yearly, (C) produced once every two years.

3.3.2.3 *Validation of growth*: Diver based observations during March-April at Arch Rock and other adjacent sites in the Huon region indicated that there were two distinct juvenile cohorts visible, one with a mean size of approximately 6 cm, the other with mean size of approximately 12 cm total length. Subsequent ageing of individuals collected from these cohorts in April showed no growth ring for individuals of the 6 cm cohort (0+ years) and only one growth ring in all individuals assigned by their length to be in the 1+ year class (Fig 3.7). These observations appear to validate the reliability of otolith growth rings for ageing, at least in the first year of growth.

To assess the validity of ageing based on two or more rings, the von Bertalanffy value of length at age of the 3+ cohort of Fig. 3.7 was used to predict the mean length of ages 4+ onwards from the Ford-Walford relationship in Fig. 3.5A. The year 3+ was chosen as the starting point because that length (17.9 cm) was close to the length at which the data from which the model was derived started. The resulting growth curve was compared with three von Bertalanffy curves based on the assumptions of otolith growth rings being produced twice yearly, once yearly, and once every two years (Fig. 3.8). There was a very good fit between the growth curve derived from tagging and the curve based on otolith increments of one per year, indicating that these rings are probably annual and may be a valid method of ageing this species. The predicted lengths at age for 4+ to 13+ year classes were exceptionally close to those derived from the von Bertalanffy growth curve, although the curves diverged after this, resulting in a difference equivalent to 2 years growth after 17 years. As an example of the problems associated with fitting models to such data sets, I have included the length at age growth curve predicted from recaptures in 1990-91 and 1991-92. This curve fits the age based von Bertalanffy curve almost perfectly (Fig. 3.9)(where the length based model is  $y = 0.8946x + 4.4068$ ). With the addition of recaptures in 1992-93 (only 12 fish) this curve changed to that shown in Fig. 3.8A.

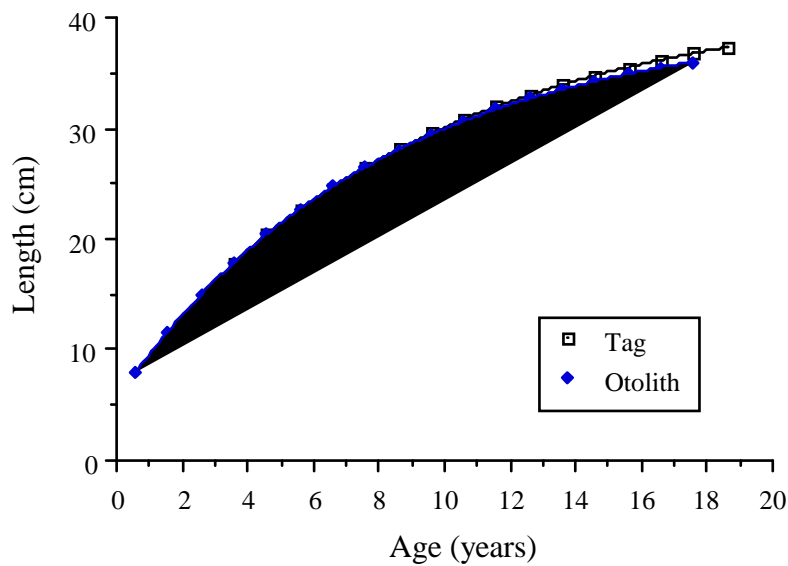


Figure 3.9 Comparison of *Notolabrus fucicola* Huon survey otolith based growth curve with the curve derived from tag based growth of fish tagged and recaptured fish between May 1990 and January 1993.

3.3.2.4 *Sex-related growth*: The relationship between sex and growth was examined from two surveys where the sex of a sufficient number of individuals had been histologically determined. These surveys were from Ninepin Point in September 1990 and the East Coast sites in February 1994. Comparison of age based growth rates was by ANCOVA of untransformed data. The data was not transformed before analysis as residual plots indicated no obvious heteroscedasticity, and a near normal distribution of residuals. The results (Table 3.3) indicated that there was no evidence to suggest a sex related difference in growth, as both elevation (Sex) and slope (Sex by Age interaction) terms remained non-significant at both sites.

Table 3.3 Results of a test of differences between the growth rates of male and female *Notolabrus fucicola*, collected during the Ninepin Point (September 1990) and East Coast (February 1994) growth rate surveys and aged by counting otolith annuli. Growth rates were compared by ANCOVA of the length at age relationship. Test 1 is a test of slopes (sex\*age) and elevation (sex). Test 2 is a test of elevation with the slope term removed (once it is identified as non-significant by test 1).

Site	Test	Source	df	SS	MS	F	P
Ninepin Point	1	Age	1	65378	65379	0.147	< 0.01
"	1	Sex	1	16.0	16.0	0.04	0.85
"	1	Sex*Age	1	99.5	99.5	0.23	0.64
"	1	Error	45	19931	443		
"	2	Age	1	67160	67161	154	< 0.01
"	2	Sex	1	397	397	0.91	0.35
"	2	Error	46	20031	436		
East Coast	1	Age	1	2114	2114	0.464	< 0.01
"	1	Sex	1	12.1	12.1	2.64	0.11
"	1	Sex*Age	1	5.82	5.82	1.28	0.26
"	1	Error	79	360	4.5		
"	2	Age	1	2440	2440	0.533	< 0.01
"	2	Sex	1	9.36	1	9.36	0.16
"	2	Error	80	4.57			

### 3.3.3 *Pictilabrus laticlavius*

3.3.3.1 *Tag based growth estimates:* *Pictilabrus laticlavius* was abundant at Arch rock for the duration of the study period; however individuals rarely entered traps. Of the 183 individuals tagged during the study, only 26% were subsequently recaptured, with only 16 fish being recaptured within the 10-14 month window after tagging required for reliable estimation of annual growth rates. Many of the recaptured fish had lost their tags, probably due to the crepuscular nature of this species. The recapture data are presented in Fig. 3.10A, a Ford-Walford plot showing the estimated length one year after tagging plotted against length at tagging for fish initially tagged in the size range 15.5-26.5 cm total length. The relationship over this size range was best modelled by the linear regression  $y = 6.89 + 0.7216x$ , which fitted the data ( $r^2=0.96$ ).

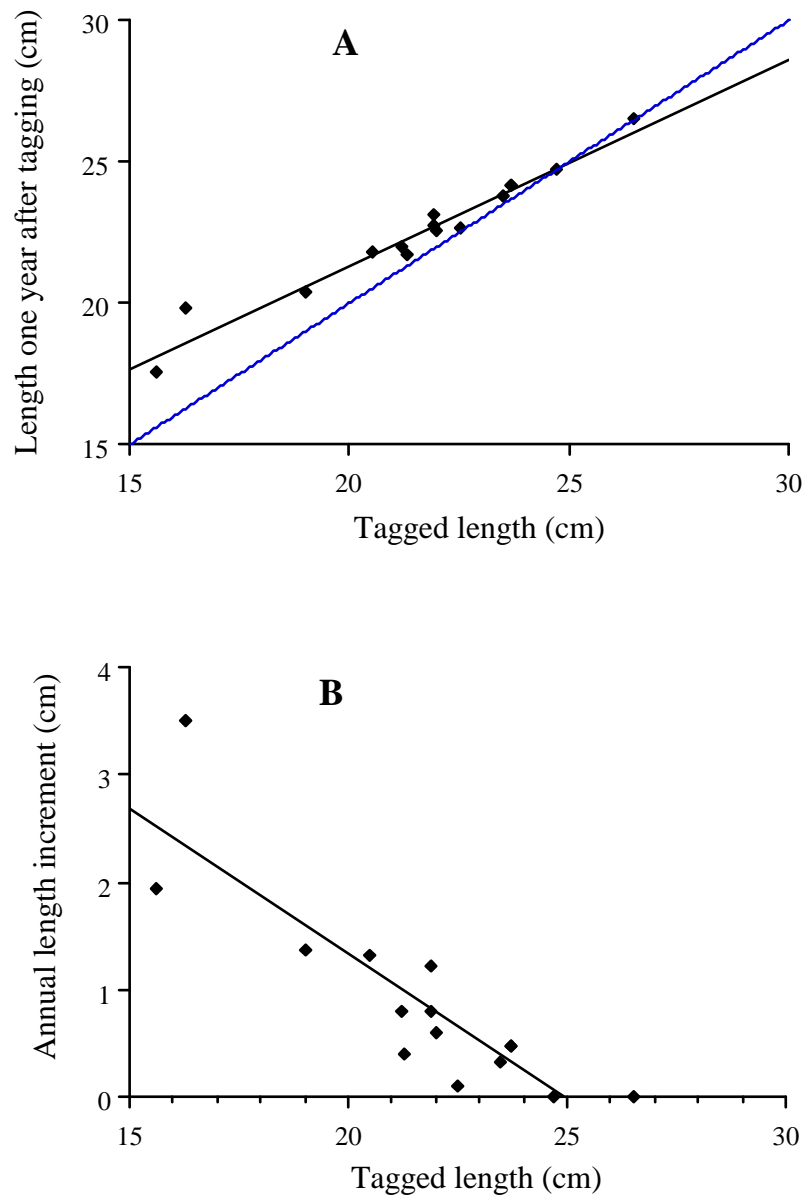


Figure 3.10 Annual growth data from 15 *Pictilabrus laticlavius* tagged and recaptured at Arch Rock, Tasmania, between May 1990 and January 1994. Presented as (A), a Ford-Walford plot of length at tagging against length one year after tagging (with unity line fitted), and as (B), a Manzer-Taylor plot of annual length increment against tagged length.

Many fish were captured over shorter and longer periods than 12 months, and the growth trajectories of some of these individuals are shown in Fig. 3.11. This figure

indicates that there was a considerable degree of intra-specific variation in growth rate, and that these differences may continue over long time frames, in excess of 12 months. The von Bertalanffy growth parameters  $L_{\infty}$  and  $K$  were estimated from the length increment data by least squares estimation (Table 3.1) giving  $L_{\infty} = 24.7$  cm, and  $K = 0.33$ , results confirmed from the Manzer-Taylor plot (Fig 3.10B). The Manzer-Taylor plot also highlights the variability in growth between individuals, although this variability does not appear to be of the same order of magnitude as that found in *Notolabrus tetricus* and *N. fucicola*, species in which growth rates are much faster at the lengths shown here.

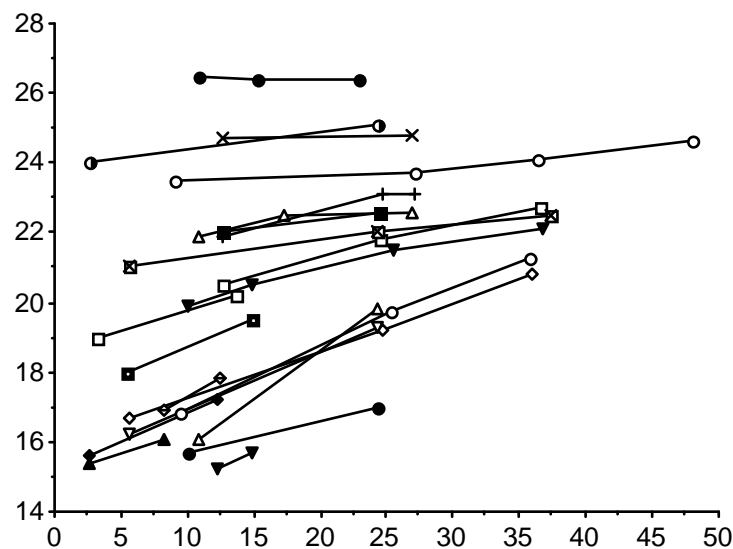


Figure 3.11 Growth trajectories of a selection of *Pictilabrus laticlavius* individuals tagged and recaptured at Arch Rock between May 1990 and January 1994.

**3.3.3.2 Otolith based growth estimates:** To estimate the length at age relationship for *P. laticlavius*, 21 fish were collected over as wide a size range as possible in the Huon region in April 1993. Ages were determined from what appeared to be annual growth rings in sagittal otoliths. These rings were usually better defined than those in otoliths of *N. fucicola* and *N. tetricus*. Like the other labrids, the radius to the first ring was highly variable between individuals and probably reflects the consequence of an extended

breeding season, with the subsequent recruits for each year class potentially varying by as much as 4 months growth. The von Bertalanffy growth parameters  $L_{\infty}$ ,  $K$  and  $T_0$  were estimated (Table 3.2) and the von Bertalanffy growth curve derived from these was fitted to the raw length at age data (Fig. 3.12,  $r^2 = 0.66$ ). The predicted value for  $L_{\infty}$  of 24.5 cm was very close to that estimated from the recapture data set (24.8 cm).

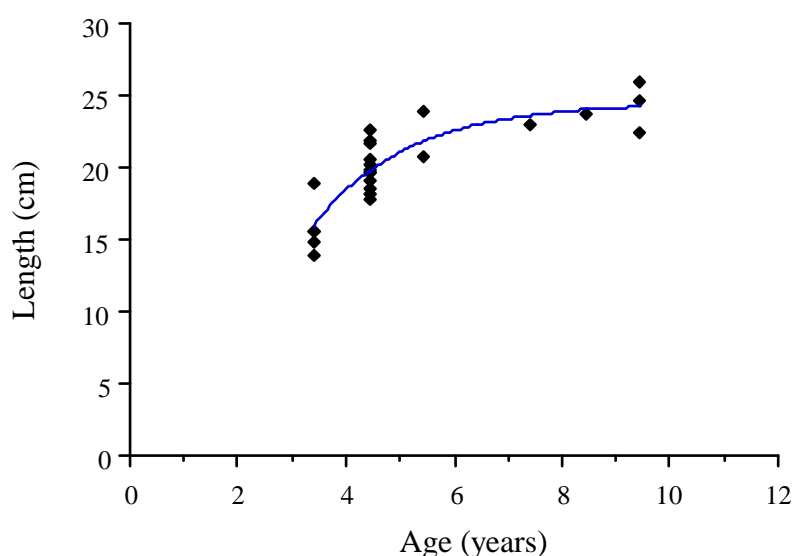


Figure 3.12 *Pictilabrus laticlavius* length at age relationship, for fish collected in the Huon survey (April 1993) and aged from counts of otolith annuli. The von Bertalanffy growth curve is fitted. Age is based on the assumption of a September 1 birthdate.

The data points of Fig. 3.12 are heavily concentrated on the 4+ year class with few other classes being well represented. Because it was possible that a growth curve derived from such poorly distributed data points might not be truly representative of growth in this species, the Huon region curve was compared with that obtained from 50 fish collected in the East Coast survey in February 1994 (Fig. 3.13). Fish collected from the various sites within this survey were able to be pooled because growth was shown to be similar between sites (see Chapter 6). Fish collected from the East Coast had a much more representative spread of age classes (Fig 3.13), and included representatives of the 1+ and 2+ classes which were missing from the Huon collection. The von Bertalanffy growth parameters  $L_{\infty}$  and  $K$  derived from the East Coast survey were  $24.7 \pm 0.3$ (s.e.)



and  $0.46 \pm 0.04(\text{s.e.})$ , and were close to those obtained for growth of fish in the Huon region (Table 3.2). A comparison of growth between the two survey sites by ANCOVA detected no significant differences in either slope or elevation (Table 3.4), indicating that the growth rates are similar between regions. The maximum age determined for this species by otolith ageing was 11.5 years (Fig. 3.13).

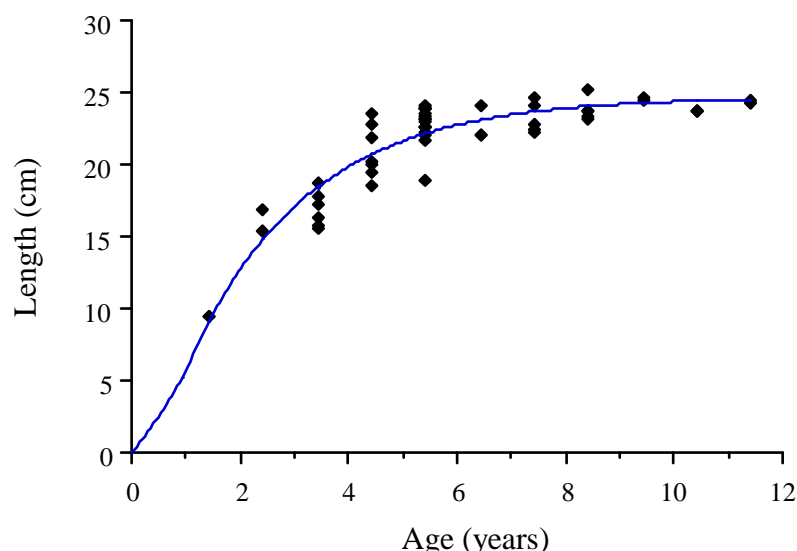


Figure 3.13 *Pictilabrus laticlavius* length at age relationship, for fish collected in the East Coast survey (February 1994) and aged from counts of otolith annuli. The von Bertalanffy growth curve is fitted. Age is based on the assumption of a September 1 birthdate.

Table 3.4 Comparison of growth of *Pictilabrus laticlavius* in the Huon region with that from the East Coast based on fish collections made in February 1994 (East Coast,  $n = 48$ ) and April 1993 (Huon,  $n = 20$ ), and aged from otolith annuli. Growth rates were compared by ANCOVA of the length at age relationships. Test 1 is a test of slopes (sex\*age) and elevation (sex). Test 2 is a test of elevation with the slope term removed (once it is identified as non-significant by test 1).

Test	Source	df	SS	MS	F	P
1	Age	1	234	234	51.3	< 0.01
1	Site	1	0	0	0	1.00
1	Age*Site	1	0.14	0.14	0.03	0.86
1	Error	64	292	4.55		
2	Age	1	349	349	77.7	< 0.01
2	Site	1	0.89	0.89	0.20	0.66
2	Error	65	292	4.49		

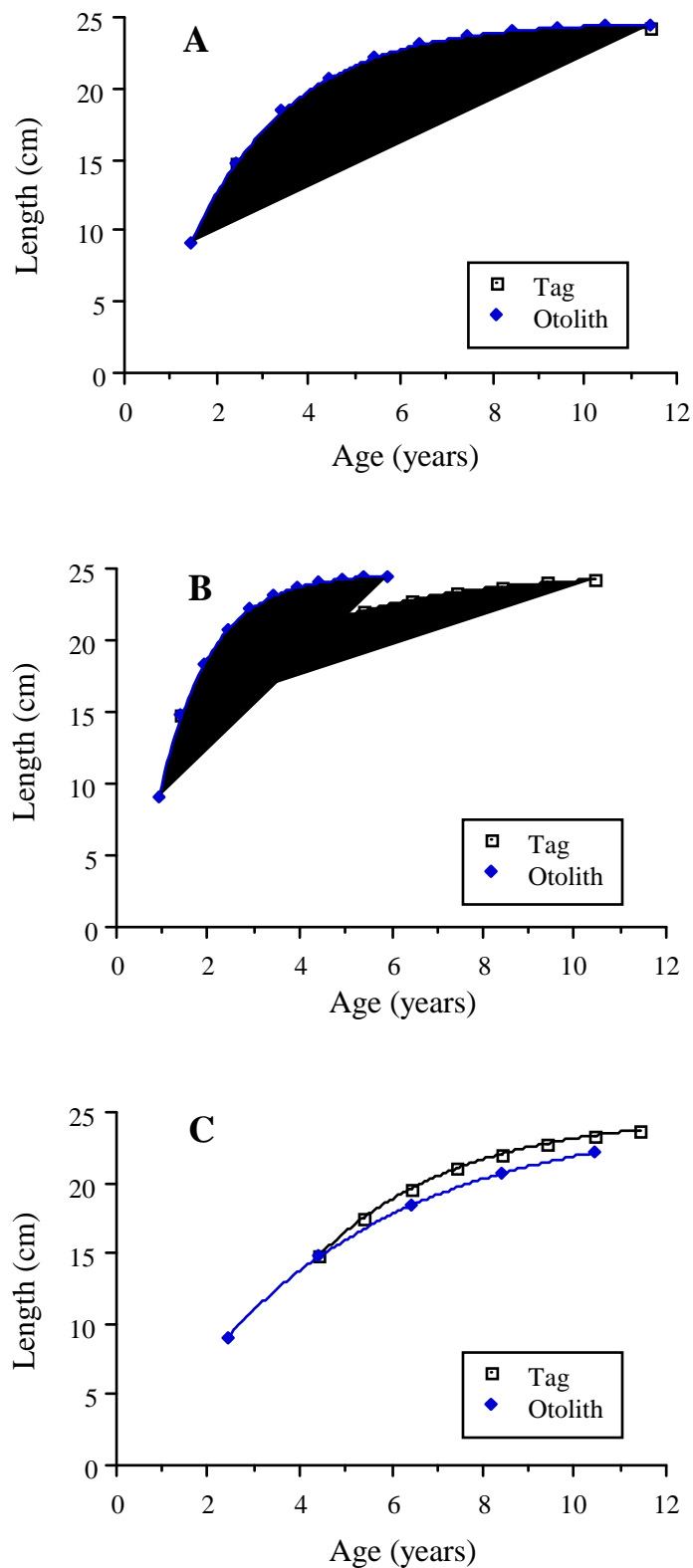


Figure 3.14 Comparison of the growth curve of *Pictilabrus laticlavius* tagged at Arch Rock, with the von Bertalanffy curves derived from fish collected in the East Coast survey (February 1994) and aged from otolith annuli under three assumptions, (A) annuli are annual, (B) produced twice yearly, (C) produced once every two years.

3.3.3.3 *Validation*: Unlike *N. tetricus* and *N. fucicola* where the 0+ and 1+ cohorts were readily identifiable and able to be collected, *P. laticlavius* juveniles are exceptionally cryptic in their coloration and behaviour, and individuals less than 9 cm were never sighted, despite intensive searches. Validation of growth was therefore limited to individuals of 16 cm total length and above. To assess the validity of the otolith-based growth estimates, the mean length at age of the 2+ cohort of the East Coast survey was used to predict the length at age relationship of years 3+ and onwards, from the tag based Ford-Walford growth relationship of Fig. 3.10A. This method was also used to predict the length at age relationship in the Huon region, using the mean length at age of the 3+ cohort from the Huon Collection as the starting point. The 3+ cohort was used as no 2+ individuals were collected in the Huon Survey. The resulting growth curves were each compared with the von Bertalanffy curves obtained from otolith ageing (Figs 3.14 and 3.15).

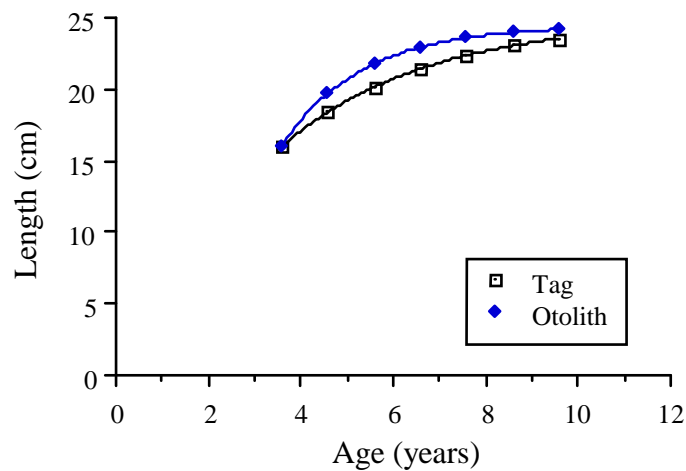


Figure 3.15 Comparison of the growth curve of *Pictilabrus laticlavius* tagged at Arch Rock, with the von Bertalanffy curve derived from fish collected in the Huon region survey (April 1993) and aged from otolith annuli under the assumption that annuli are annual.

For the East Coast survey, the length at age curve derived from tag based growth was compared with three possible von Bertalanffy curves, assuming growth rings are produced twice per year, once per year, or once every two years (Fig. 3.14). This comparison was made with the East Coast data rather than the Huon data because of the greater number of replicates at the latter site. In this comparison the best fit was obtained from the assumption of one growth ring per year, indicating that these rings are almost certainly produced annually. With the assumption of one increment per year, the two growth curves were very similar for the East Coast survey comparison, and never diverged by more than one years growth over the age range of 2 - 11 years, indicating that age estimates based on otolith growth rings may be reliable. The two curves from the Huon region growth comparison (Fig 3.15) was not as close a fit as those from the East Coast; however, it is likely that the von Bertalanffy curve calculated for this site from the otolith ageing data is not a true representation of the real growth curve because of the limited data available for calculation of the von Bertalanffy parameters.

### 3.3.4 *Pseudolabrus psittaculus*

3.3.4.1 *Tag based growth estimates*: This species was the least abundant of the labrids at Arch Rock, primarily due to the restricted availability of its preferred habitat, which at Arch Rock was dissected reef at depths of 7 m and greater. However, recapture rates were high, and of the 85 individuals tagged, 44 of these were subsequently recaptured during the 10-14 month period after tagging required for useful estimation of annual growth. A Ford-Walford plot derived from fish caught 10-14 months after tagging, is shown in Fig 3.16A. The growth relationship shown in this plot is represented by the linear regression  $y = 2.85 + 0.9138x$  ( $r^2 = 0.91$ ).

The von Bertalanffy growth parameters  $L_\infty$  and  $K$  (Table 3.1) were estimated from the length increment data by least squares estimation revealing an  $L_\infty$  of  $33.0 \pm 9.8$  (s.e.), and an estimate of  $K$  of  $0.090 \pm 0.059$  (s.e.). These high error margins reflect on the

accuracy of the estimates, and may be at least partly the result of insufficient data at the extremes of fish sizes, and highly variable individual growth rates. The Manzer-Taylor plot of annual length increment against length at tagging (Fig. 3.16B) highlights the variability in growth rate within this species.

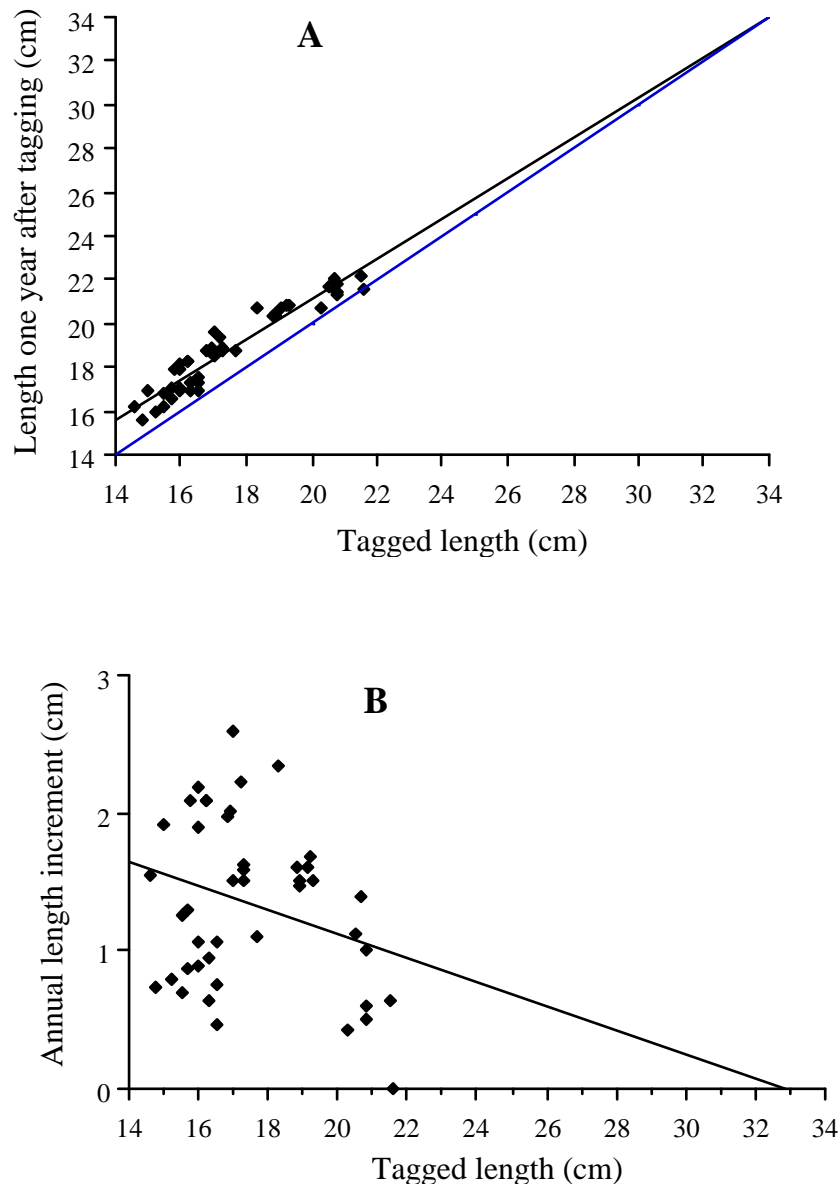


Figure 3.16 Annual growth data from 44 *Pseudolabrus psittaculus* tagged and recaptured at Arch Rock, Tasmania, between May 1990 and January 1994. Presented as (A), a Ford-Walford plot of length at tagging against length one year after tagging (with unity line fitted), and as (B), a Manzer-Taylor plot of annual length increment against tagged length.

The growth trajectories of a random selection of the recaptured fish are shown in Fig. 3.17; some of these fish were at large for over of 40 months. The difference in the slope of the growth trajectories indicates that there is a considerable degree of intra-specific growth variability and that this difference in growth rate may continue over long time frames ( $\geq 12$  months).

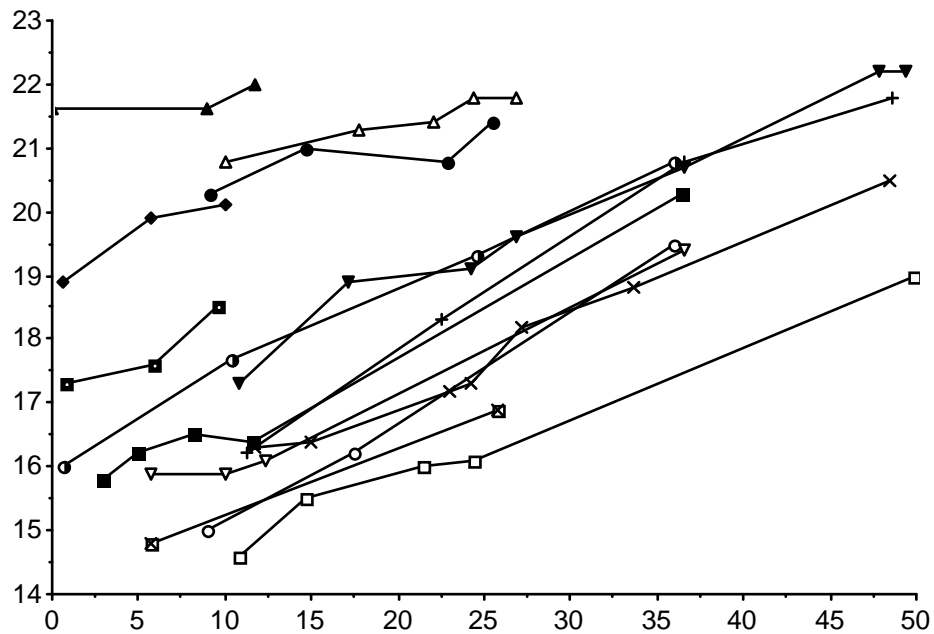


Figure 3.17 Growth trajectories of a selection of *Pseudolabrus psittaculus* individuals tagged and recaptured at Arch Rock between May 1990 and January 1994.

**3.3.4.2 Otolith based growth estimates:** To estimate the length at age relationship for *P. psittaculus*, 20 fish were collected over as wide a size range as possible from the Huon region in April 1993. Ages were determined from what appeared to be annual growth rings in sagittal otoliths. Like the other labrids examined, and probably for the same reason, the radius to the first growth ring was highly variable. From these otoliths the von Bertalanffy growth parameters  $L_{\infty}$ ,  $K$  and  $T_0$  were estimated (Table 3.2), and the resulting von Bertalanffy curve derived from these estimates is shown in Fig 3.18 ( $r^2 = 0.91$ ). The estimated  $L_{\infty}$  of 22.5 cm was close to that observed for the region that calculated from the recapture data (33.0 cm). The data points of Fig. 3.18 were heavily

concentrated in the 1+ and 5+ year classes, possibly due to the abundance of these year classes, and some bias associated with the collection methods.

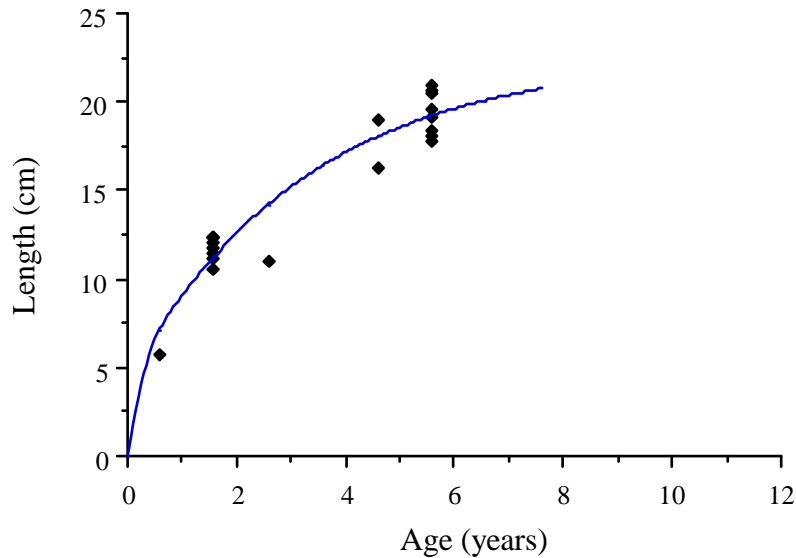


Figure 3.18 *Pseudolabrus psittaculus* length at age growth data, for fish collected in the Huon region survey (April 1993) and aged from counts of otolith annuli. The von Bertalanffy growth curve is fitted. Age is based on the assumption of a September 1 birthdate.

Because it was possible that the growth curve defined by this data distribution might not be truly representative of growth in this species, the growth curve derived from 48 fish collected from the East Coast survey in February 1994 (Fig. 3.19) was also examined. Fish collected from the various sites within this survey were able to be pooled because growth was shown to be similar between sites (see Chapter 6). Figure 3.19 has a much more representative spread of age classes, including numerous ages missing from the Huon sample. The von Bertalanffy growth parameters were estimated to be  $L_{\infty} = 25.83 \pm 1.6(\text{s.e.})$ ,  $K = 0.22 \pm .05(\text{s.e.})$ . A comparison of growth at the two "sites" by ANCOVA (Table 3.5) found that the regressions describing growth had significantly different slopes (site by age interaction,  $p = 0.003$ ) reflecting different growth rates. The East Coast curve cannot therefore be used to represent growth in the Huon region, but it is still useful as an indication that the shape of the curve fitted to the Huon data

approximates the correct one. The maximum age of this species from otolith ageing was 10.5 years, recorded from the East Coast collection (Fig 3.19).

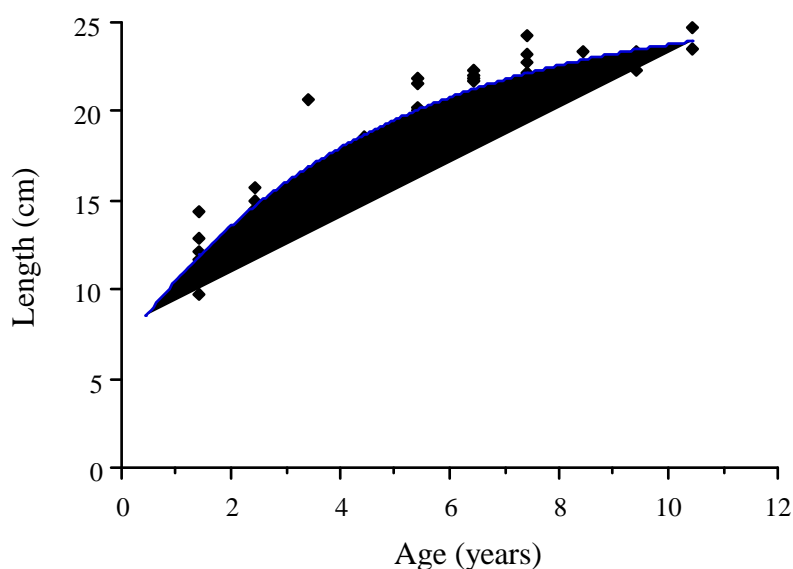


Figure 3.19 *Pseudolabrus psittaculus* length at age relationship, for fish collected in the East Coast survey (February 1994) and aged from counts of otolith annuli. The von Bertalanffy growth curve is fitted. Age is based on the assumption of a September 1 birthdate.

Table 3.5 Comparison of growth of *Pseudolabrus psittaculus* in the Huon region with that from the East Coast based on fish collections made in February 1994 (East Coast, n = 48) and April 1993 (Huon, n = 18), and aged from otolith annuli. Growth rates were compared by ANCOVA of the length at age relationships.

Source	df	SS	MS	F	P
Age	1	759	759	290	< 0.001
Site	1	31.2	31.2	11.9	0.001
Age*Site	1	25.1	25.1	9.6	0.003
Error	62	163	2.62		

3.3.4.3 *Validation*: Two distinct cohorts of *Pseudolabrus psittaculus* were evident from diving surveys of the Huon region in April 1993 when fish were collected. These were of newly arrived recruits of approximately 6 cm total length, and another distinct group



of approximately 10 cm total length. Only one individual of the 6 cm class was collected; and there was no growth check on its otolith. Nine individuals in the 10 cm class were collected and all were found to have one growth check, thus validating the use of otolith growth marks for ageing young fish of this species. To assess the validity of the age based growth estimates for fish in excess of 2+ years, the mean estimated length at age of the 2+ cohort was used to predict the mean length at age of ages 3+ and upwards, from the Ford-Walford growth relationship (Fig. 3.16A). The length at 2+ years was chosen as the starting point as it represents a length covered by the data from which the model was derived. The resulting growth curve was then compared with the von Bertalanffy curves obtained from otolith ageing, assuming growth rings were produced twice yearly, yearly, and once every two years (Fig 3.20). There was a good fit with the curve based on one ring per year, suggesting that of the three possibilities, annual rings are the most likely. The two annual growth curves only ever differed by a length equivalent to half a years growth between the ages of 3+ and 7+, suggesting growth checks are annual and that they can be used to age this species reliably.

### 3.3.5 *Penicipelta vittiger*.

3.3.5.1 *Introduction*: This species was relatively common at Arch Rock and over the duration of the study period 214 fishes were tagged. However, most individuals were trap shy, with a mean number of recaptures per individual of only 0.8 (Table 2.5). This lack of attraction to traps, combined with a high rate of tag loss (probably associated with the short life span of this species) meant that there were few recaptures over a 10-14 month period, the time window necessary to gain a reasonable estimate of annual growth. This problem was further compounded by the fact that growth of males and females had to be considered separately, as a comparison of the sex related growth curves of this species (derived from otolith aged fish collected during the East Coast

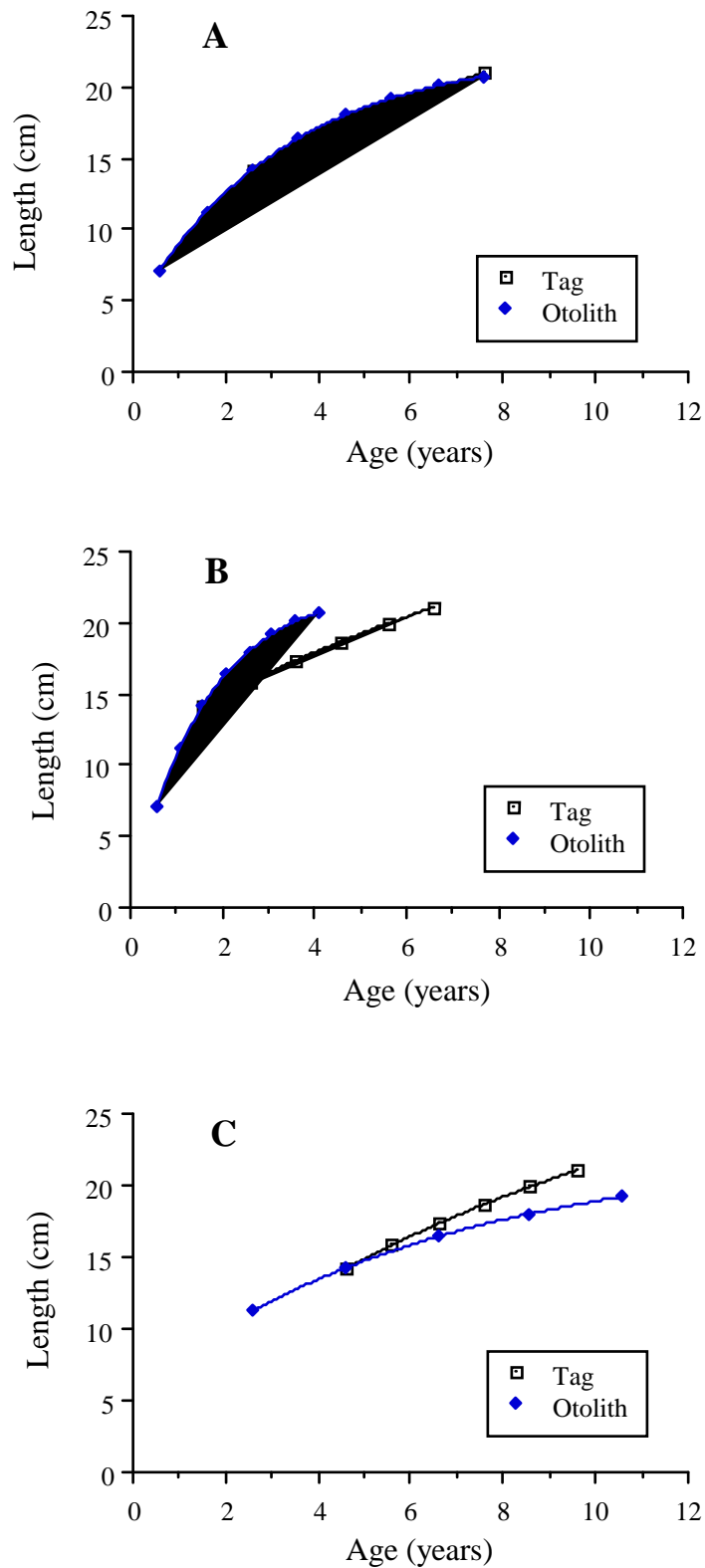


Figure 3.20 Comparison of the growth curve of *Pseudolabrus psittaculus* tagged at Arch Rock, with the von Bertalanffy curves derived from fish collected in the East Coast survey (February 1994) and aged from otolith annuli under three assumptions, (A) annuli are annual, (B) produced twice yearly, (C) produced once every two years.

survey) found them to be significantly different (Sex x Age interaction,  $p < 0.001$ , Table 3.6). This comparison was by ANCOVA of untransformed data. The data were not transformed as the residuals plot indicated the data to be normally distributed with no obvious heteroscedasticity.

Table 3.6 Results of a test of differences between the growth of male ( $n = 61$ ) and female ( $n = 71$ ) *Penicipelta vittiger*, collected during the East Coast (February 1994) growth rate survey and aged by counting otolith annuli. Growth rates were compared by ANCOVA to examine slope and elevation effects on the length at age relationship.

Source	df	SS	MS	F	P
Age	1	1498	1498	700	$< 0.001$
Sex	1	11.0	11.0	5.3	0.025
Age*Sex	1	31.8	31.8	14.8	$< 0.001$
Error	126	270	2.14		

### 3.3.5.2 Males

3.3.5.2.1 *Tag based growth estimates*: Only four recaptures were made in the 10-14 month period after tagging, and therefore a Ford-Walford plot could not be constructed. These recaptures are instead shown in Table 3.7. The growth trajectories of all 14 recaptured males are presented in Fig. 3.21, and show that growth is initially fast until a length of approximately 27 cm is reached, after which growth slows substantially.

Table 3.7 Annual growth estimates of four *Penicipelta vittiger* males tagged and recaptured at Arch Rock, Tasmania, between May 1990 and January 1994.

Tagged length (cm)	Estimated length after one year (cm)
20.0	25.6
22.8	29.6
24.2	29.5
28.0	29.3

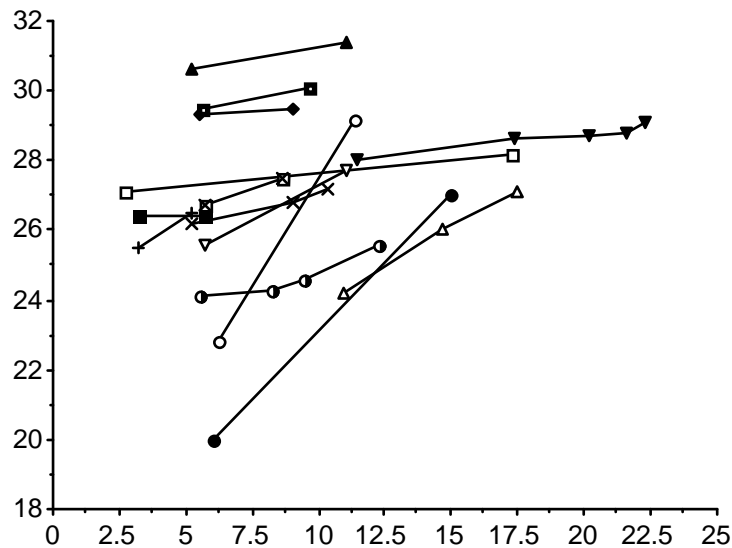


Figure 3.21 Growth trajectories of *Penicipelta vittiger* males tagged and recaptured at Arch Rock between May 1990 and January 1994.

3.3.5.2.2 *Otolith based growth estimation*: Despite an extensive search, only 6 males of this species were able to be collected in the Huon region survey for estimation of age based growth (Fig. 3.22), and this sample is too small to accurately define the growth curve at this location. To help aid interpretation of growth in the Huon region, the growth curve obtained from 72 males collected in the East Coast survey in February 1994 was also examined (Fig. 3.23). Ages were determined from what appeared to be annual growth rings in the sagittal otoliths. In a similar manner to the labrids, the radius to the first growth ring varied substantially between individuals and was probably a result of the extended spawning season observed in this species (August to January). The von Bertalanffy parameters were not able to be estimated from this data as the iterative model used was unable to converge on an estimate.

The mean length of the 2+ cohort from the East Coast sites was  $26.36 \pm 0.24$  ( $n = 51$ ), and when compared by t - test was not significantly different from the mean length at age 2+ of  $28.0 \pm 1.79$  ( $n = 6$ ) for the Huon region survey ( $p = 0.09$ ). If the mean length

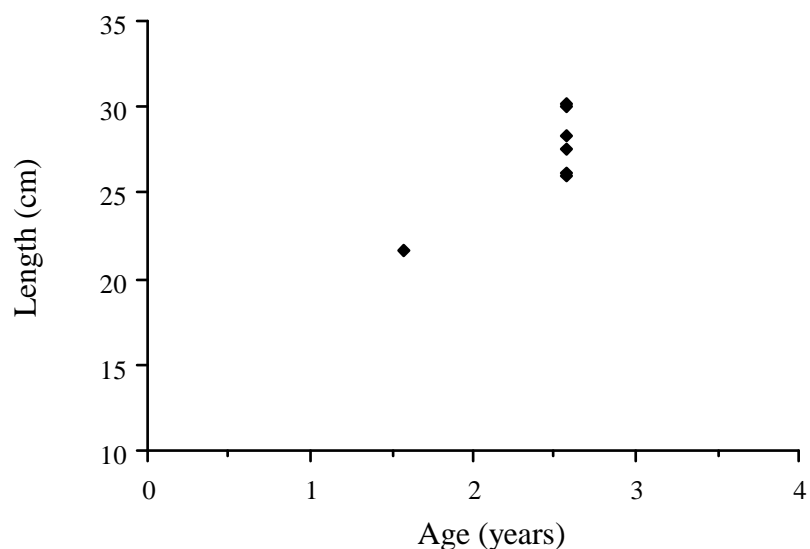


Figure 3.22 *Penicipelta vittiger* male length at age relationship for fish collected in the Huon region survey (April 1993) and aged from counts of otolith annuli.

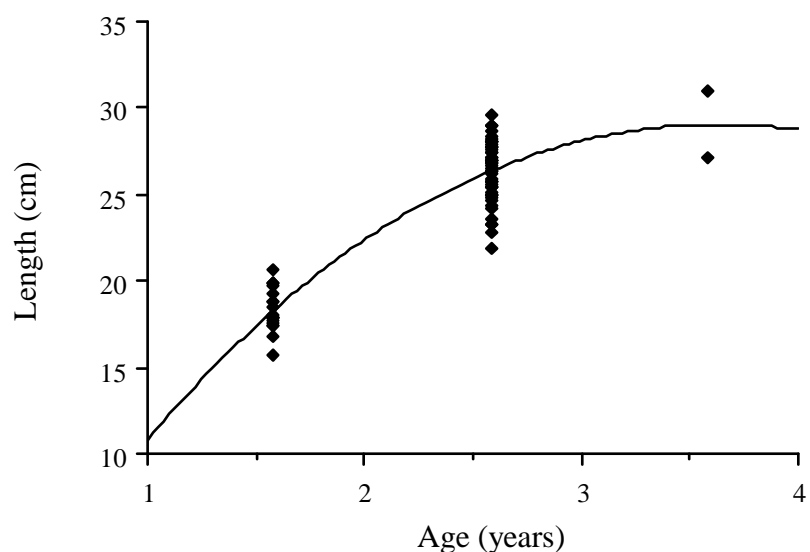


Figure 3.23 *Penicipelta vittiger* male length at age relationship for fish collected in the East Coast survey (February 1994) and aged from counts of otolith annuli.

of the East Coast fish is adjusted for the two month difference in growth between the two surveys, then the equivalent April mean length of 2+ East Coast fish would be 27.7 cm, a value almost identical to that found in the Huon survey, and indicating that growth in the two regions is very similar. The maximum age of males of this species

determined from otolith ageing was 3.5 years, although few males appear to survive to this age (Fig 3.23).

**3.3.5.2.3 Validation:** In the Huon region in April 1993 a distinct 0+ age class of *Penicipelta vittiger* was evident. At Arch Rock these appeared as schools of juveniles inhabiting shallow (0-5 m) *Phyllosphora comosa* forests at the western end of the island. While none could be collected for ageing, their mean length was estimated to be 6 cm with a range of  $\pm 2$  cm. These schooling juveniles were quite distinct at Arch Rock from the first obvious group of males, which were solitary and more sedentary. These males were probably not reproductively active as they did not court females, and were not brightly coloured and lacked the toothbrush like spines of mature males. The length of fish in this group was estimated in April 1993 as 14-20 cm. The next distinct group observed was that of brightly coloured and reproductively active males, with distinct toothbrush-like spines on their sides between the soft dorsal and anal fins. Members of this group, which ranged in size from 24-30 cm in length, were observed actively courting females throughout the spawning season. These behaviourally distinct groups correlate well with those identified from otolith ageing (Figs 3.22 and 3.23) which indicate that there are several distinct cohorts, with a 1+ cohort centred around 18 cm length and a 2+ cohort centred around 26 cm in length. The tagging data (Table 3.7 and Fig. 3.21) indicates that a fish of 20 cm length (within the 1+ age class) can easily grow to 26 cm or more in one year, and that thereafter growth may slow considerably, perhaps being related to the onset of sexual maturity. This observed growth pattern is very similar to that predicted by otolith based estimates of growth, suggesting that counting otolith annuli may be a reliable way of ageing males of this species.

### 3.3.5.3 Females

**3.3.5.3.1 Tag based growth estimates:** The female annual growth estimates derived from tag recaptures are presented in Fig 3.24, a Ford-walford plot, however, as with the males of this species, there were insufficient data points to fit a growth model to this

data. A plot of the growth trajectories of 15 of the 20 recaptured individuals is shown in Fig 3.25, highlighting a substantial variability in individual growth rates. One individual tagged at 23.7 cm was recaptured 24 months later at 28.0 cm, indicating that females can live for at least 3 years.

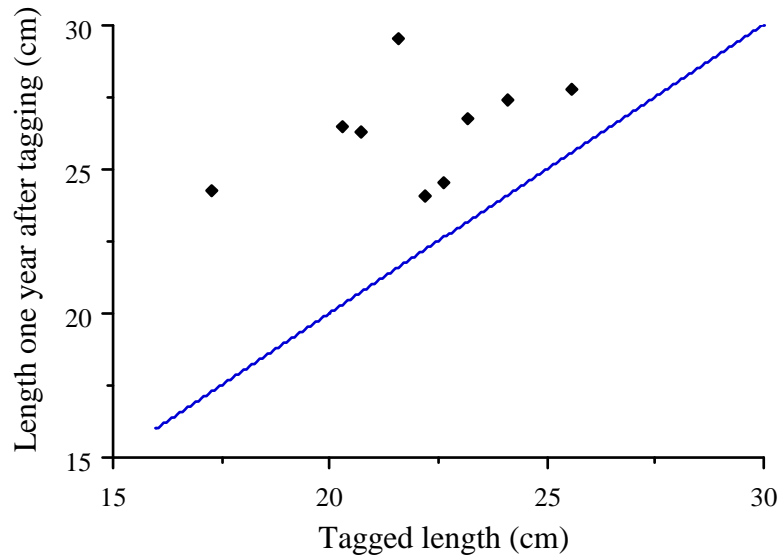


Figure 3.24 Ford-Walford plot of length at tagging against length one year after tagging, for nine *Penicipelta vittiger* females tagged and recaptured at Arch Rock, Tasmania, between May 1990 and January 1994. The unity line is fitted.

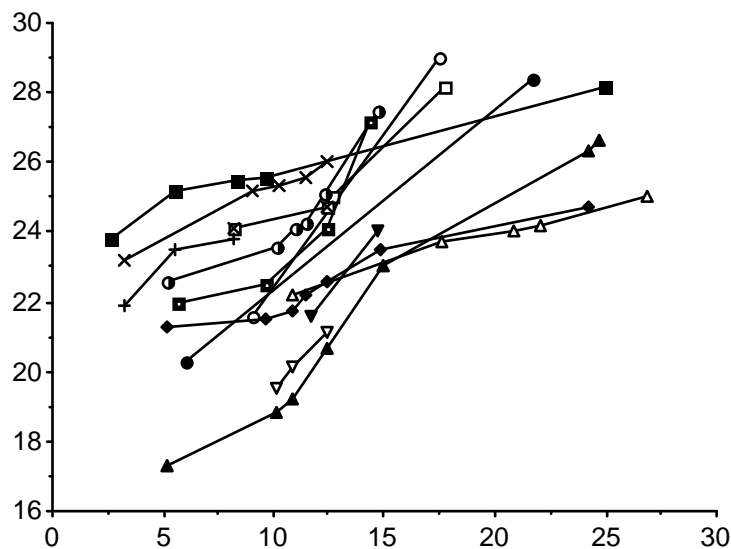


Figure 3.25 Growth trajectories of female *Penicipelta vittiger* individuals tagged and recaptured at Arch Rock. Trajectories are based on recaptures between May 1990 and January 1994.

3.3.5.3.2 *Otolith based growth estimation*: To estimate the length at age relationship for *P. vittiger* females, 30 fish were collected over as wide a size range as possible from the Huon region in April 1993. Ages were determined in a similar manner to the males of this species. The von Bertalanffy parameters  $L_{\infty}$ , K and  $T_0$  were estimated from the age-length data (Table 3.2); the von Bertalanffy curve was derived from these estimates and fitted to the raw data (Fig. 3.26,  $r^2 = 0.78$ ). Growth appeared to virtually stop at ages in excess of 3 years, although some individuals survive to 5+ years, suggesting that females may be longer lived than the males of this species.

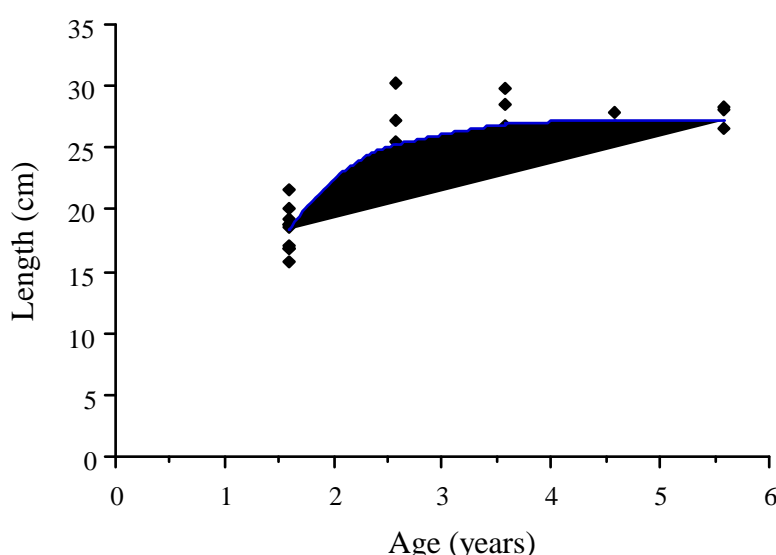


Figure 3.26 *Penicipelta vittiger* female length at age relationship, for fish collected in the Huon region survey (April 1993) and aged from otolith annuli. The von Bertalanffy growth curve is fitted.

3.3.5.3.3 *Validation*: Visual observations in the Huon region in April 1993, in particular those at Arch Rock, indicated that there were two distinct cohorts of juveniles, one of approximately 6 cm in length and the other of 14-20 cm in length. This was discussed with respect to males in the preceding section and it appears that growth of both sexes is similar for at least the first 1.5 years of growth, as the mean length of the 1+ cohort of both sexes of fish aged from otoliths was estimated at 18 cm in April. From the limited amount of tagging data available (Figs 3.24 and 3.25) it appears that an 18cm fish



would grow to approximately 24-25cm in the following year and to 26-29 cm in the year after that. These results are similar to that described by the length at age curve, assuming otolith growth rings were annual (Fig 3.26), where a 1+ cohort of mean length 18.4 cm in April, grew to 25.3 cm by 2+ and 26.9 cm by 3+, suggesting counting otolith annuli may be a valid method of ageing females of this species.

### 3.3.6 *Meuschenia australis*

**3.3.6.1 Introduction:** While *M. australis* was the least abundant of the species studied at Arch Rock, it was strongly attracted to fish traps, with 70% of tagged individuals being recaptured at least once, with each individual being recaptured, on average, nearly 10 times over the period from May 1990 to January 1994 (Table 2.5). The good recapture success meant that there was a sufficient number of recaptures of both males and females over 10-14 month periods to gain a reliable insight into annual tag-based growth in this species. It was necessary to consider the growth of each sex separately, as an analysis of the annual growth increment data from Arch Rock by ANCOVA found a highly significant effect of sex on growth rate ( $p < 0.001$ , Table 3.8). The data was not transformed as a plot of residuals showed a near normal distribution with no obvious heteroscedasticity.

Table 3.8 Results of a test of differences between the annual growth rates of male ( $n = 30$ ) and female ( $n = 42$ ) *Meuschenia australis* tagged and recaptured at Arch Rock, Tasmania between May 1990 and January 1994. Growth rates were compared by ANCOVA, examining slope and elevation effects on the length at tagging vs annual length increment relationship.

Effect	df	SS	MS	F	P
Length inc.	1	1185	1185	343	< 0.001
Sex	1	260	260	75.2	< 0.001
Length inc*Sex	1	2.70	2.70	0.78	0.38
Error	68	236	3.46		

### 3.3.6.2 Males

3.3.6.2.1 *Tag based growth estimation:* A Ford-Walford plot derived from males recaptured 10-14 months after tagging is shown in Fig 3.27A. For this species and size range, a 2nd order polynomial best described the relationship between tagged length and length one year after capture, with  $y = 30.59 - 0.75x + 0.026x^2$  ( $r^2 = 0.94$ ). This recapture data is also shown as a Manzer-Taylor plot (Fig 3.27B) to highlight the degree of variability in growth between individuals. The von Bertalanffy growth parameters  $L_\infty$  and  $K$  were estimated from the length increment data by least squares estimation (Table 3.1), giving  $L_\infty = 33.8$  cm and  $K = 0.61$ .

As well as individuals recaptured over a one year period, there were numerous recaptures over longer and shorter time frames, with times at large ranging up to 42 months. Fig. 3.28 shows a selection of the growth trajectories of individuals selected to represent the size range tagged. The differences in slopes between some of these trajectories indicates that growth rate differences between individuals can be substantial, and maintained over long time periods. It is also apparent from Fig 3.28 that there is a notable breakpoint in the rate of growth that occurs around 25-28 cm in length. Growth is rapid up to this point, after which it slows considerably.

3.3.6.2.2 *Otolith based growth estimates:* To establish the length at age relationship for male *M. australis*, 13 fish were collected over as wide a size range as possible in the Huon region in April 1993. Ages were determined from what appeared to be distinct annual growth rings in sagittal otoliths. The radius to the first growth ring was highly variable, and in a similar manner to the previously described species is probably due to the extended breeding season in this species. The age-based von Bertalanffy parameters  $L_\infty$ ,  $K$  and  $T_0$  were estimated from this data (Table 3.1), and the von Bertalanffy curve derived from these estimates was fitted to the length at age data (Fig. 3.29,  $r^2 = 0.95$ ).

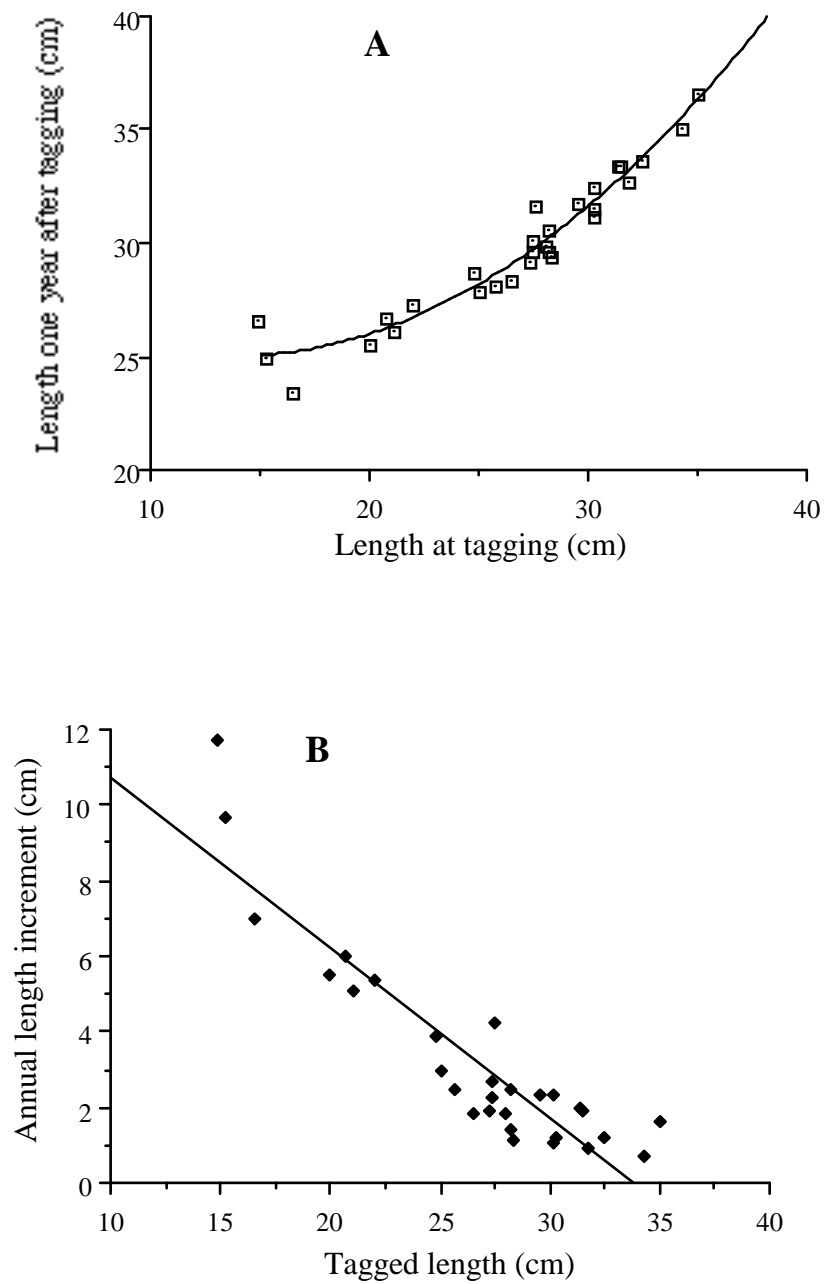


Figure 3.27 Annual growth data from 29 *Meuschenia australis* males tagged and recaptured at Arch Rock, Tasmania, between May 1990 and January 1994. Presented as (A), a Ford-Walford plot of length at tagging against length one year after tagging (fitted with a 2nd order polynomial), and as (B), a Manzer-Taylor plot of annual length increment against tagged length.

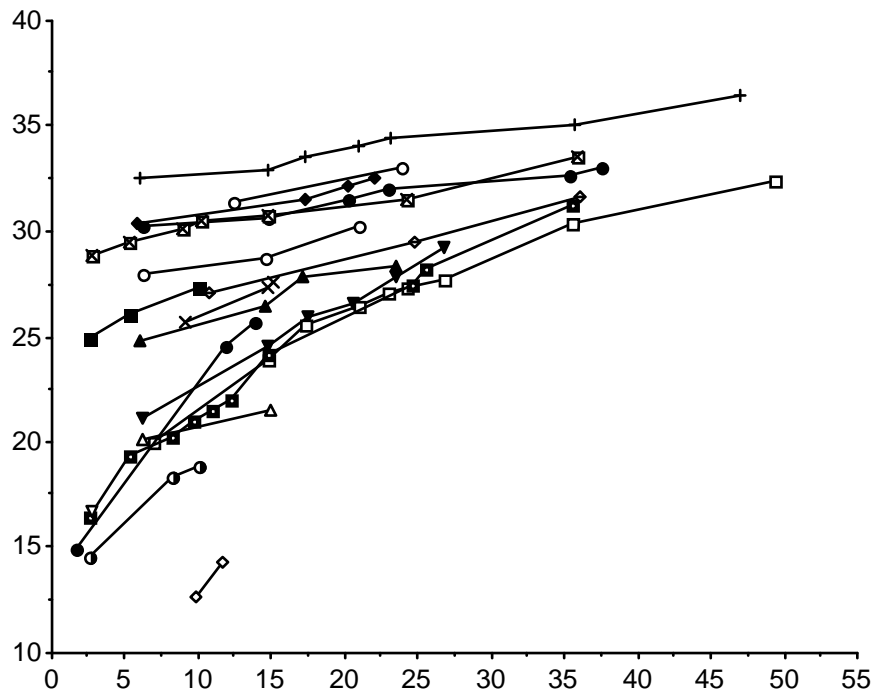


Figure 3.28 Growth trajectories of a selection of *Meuschenia australis* males tagged at Arch Rock. Trajectories are based on recaptures between May 1990 and January 1994.

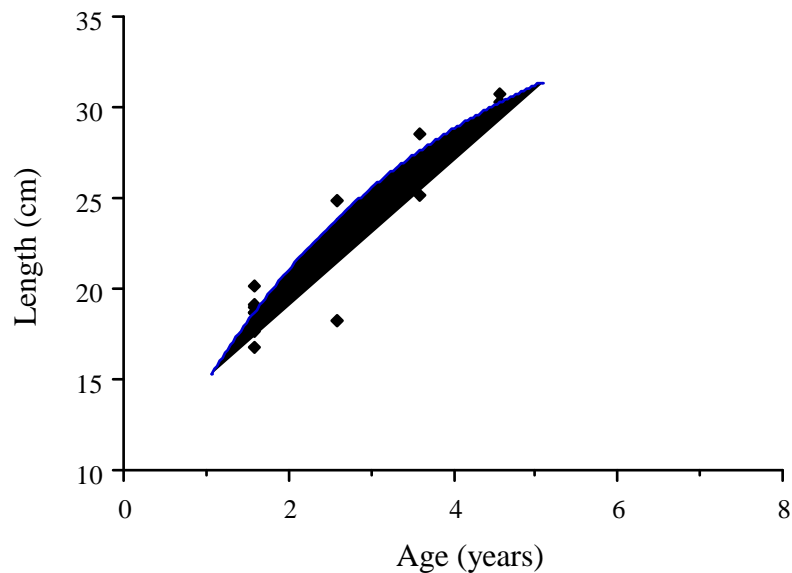


Figure 3.29 *Meuschenia australis* male length at age relationship for fish collected in the Huon region (April 1993) and aged from otolith annuli. The von Bertalanffy curve is fitted. Ages are based on the assumption of a September 1 birthdate.

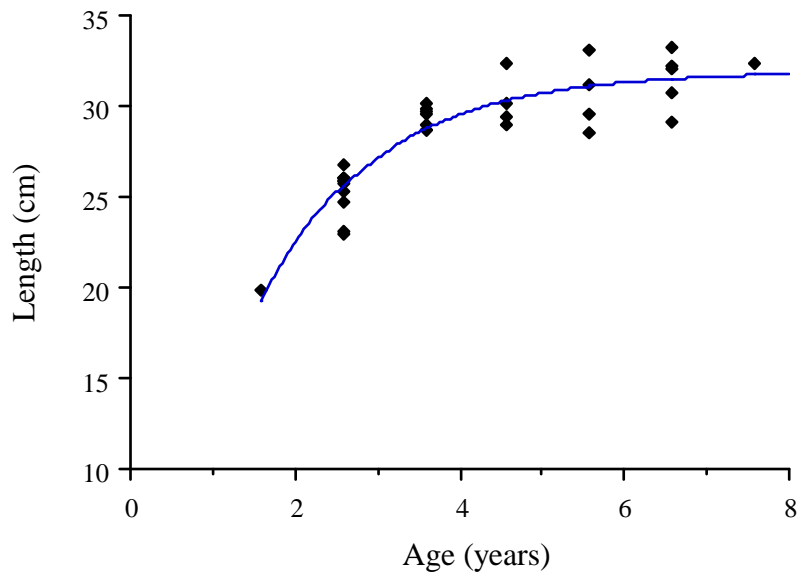


Figure 3.30 *Meuschenia australis* male length at age relationship, for fish collected in the East Coast survey (February 1994) and aged from counts of otolith annuli. The von Bertalanffy growth curve is fitted. Age is based on the assumption of a September 1 birthdate.

As only 13 fish were collected during the Huon survey, it was possible that the growth curve derived from this small data set may not adequately describe growth. To assess the validity of this curve it was compared with that obtained from fish collected during the East Coast survey in February 1994 (Fig. 3.30). A comparison of the first four year classes of the two data sets by ANCOVA (Table 3.9) indicated that there was a significant difference in slope between the growth regressions for each site ( $p < 0.001$ ), with growth in the first two years at the East Coast survey sites being faster than the Huon region. However, while growth differed between the two regions, these differences were small, and although the East Coast curve of Fig 3.30 cannot be used as a replacement for the Huon curve of Fig 3.29 it still provides an indication that the curve fitted to the Huon region data is not inappropriate. The maximum age determined from otoliths for males of this species was 7.5 years, recorded from the East Coast collection (Fig. 3.30).

Table 3.9 Comparison of growth of male *Meuschenia australis* in the Huon region with that from the East Coast, based on fish collections made in February 1994 (East Coast, n = 33) and April 1993 (Huon, n = 13), and aged from otolith annuli. Growth rates were compared by ANCOVA of the length at age relationships.

Source	df	SS	MS	F	P
Age	1	445	445	131	< 0.001
Site	1	145	145	42.8	< 0.001
Age*Site	1	81.6	81.6	24.1	< 0.001
Error	42	142	3.38		

3.3.6.2.3 *Validation*: Although the reef at Arch Rock was searched extensively for new recruits of *M. australis*, none were found until September in 1991 and 1992, when they were 12-14 cm in length. This length was approximately that expected for a 1+ year class having 9-12 months of growth. Observations on tagged individuals of this year class, as well as examination of tag based growth curves (Figs 3.27A and 3.28) indicate that this group would be in the range of 17-20 cm in length by April. In the Huon region survey in April 1993, it was found that 1+ individuals did fall into the range of 17-20 cm (Fig. 3.29), suggesting that counting of otolith growth rings may be a valid method of ageing these young fish. To assess the validity of the estimated age relationship based on two or more growth rings, the von Bertalanffy value of length of the 1+ cohort from Fig. 3.29 was used to predict the mean length of ages 2+ onwards from the length based growth relationship of Fig. 3.27A. The resulting growth curve was compared with three von Bertalanffy curves derived from the age based growth estimates (Fig. 3.31). The best fit was to the curve assuming 1 annuli per year indicating it was the most appropriate of the options, with the close fit of the tag and otolith based curves indicating that the use of otolith growth rings may provide a reliable way of ageing males of this species.

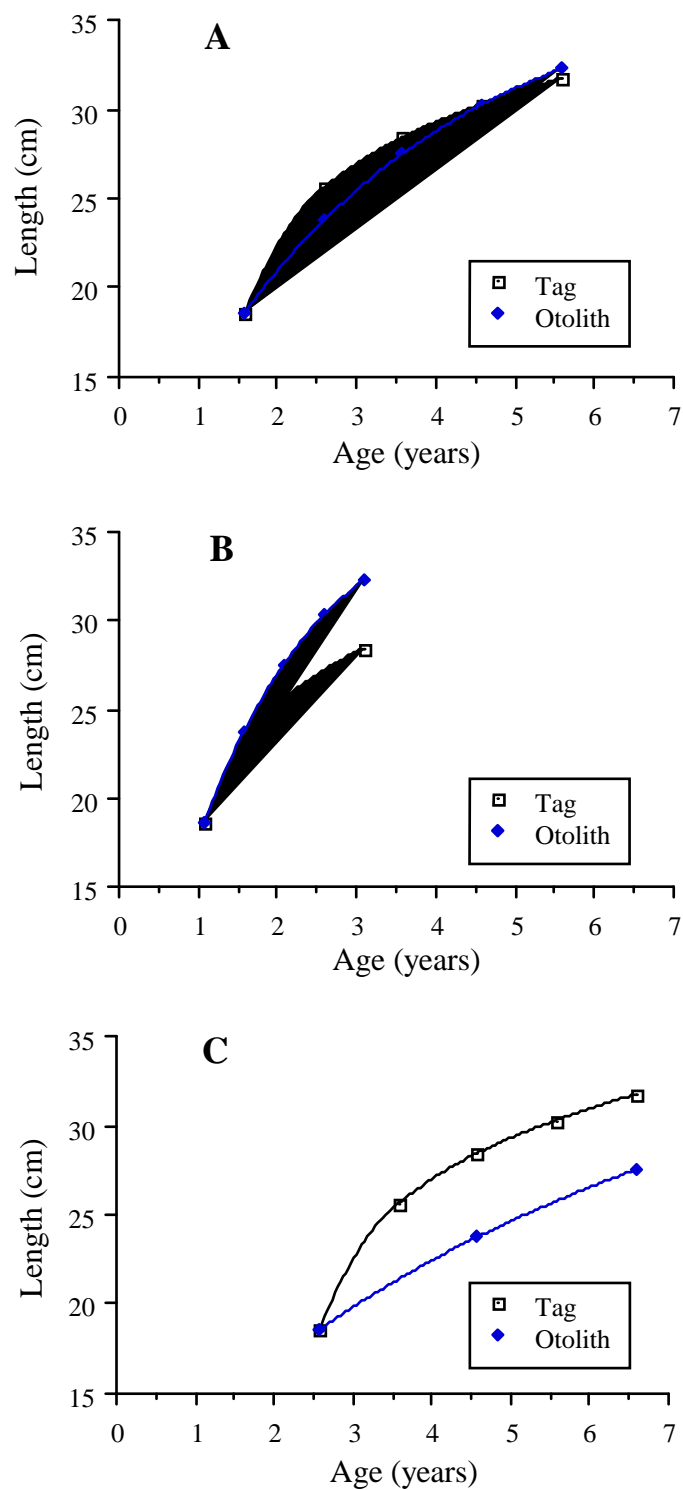


Figure 3.31 Comparison of the growth curve of *Meuschenia australis* males tagged at Arch Rock, with the von Bertalanffy curves derived from fish collected in the Huon region survey (April 1993) and aged from otolith annuli under three assumptions, (A) annuli are annual, (B) produced twice yearly, (C) produced once every two years.

### 3.3.6.3 Females

3.3.6.2.1 *Tag based growth estimation*: A Ford-Walford plot of annual growth data derived from females at large for 10-14 months is given in Fig 3.32A. For fish in the size range presented in this plot (12-29 cm) the growth relationship was best described by the second order polynomial expression  $y = 24.27 - 0.58x + 0.26x^2$  ( $r^2 = 0.90$ ) where  $x$  = length at tagging and  $y$  = length one year after tagging. The von Bertalanffy growth parameters  $L_\infty$  and  $K$  were estimated from this data by least squares estimation (Table 3.1) giving  $L_\infty = 27.3$  cm and  $K = 0.70$ . The annual length increment data is also plotted as a Manzer-Taylor plot to show the extent to which growth varies between individuals (Fig 3.32B).

Growth trajectories for 21 of the recaptured females are shown in Fig 3.33, where times at large range up to 42 months. Growth appears to be very fast between the lengths of 12 cm to approximately 22 cm, with growth over this size range taking about one year. Thereafter growth appears to slow considerably, with the length at which growth slows probably being determined by the onset of sexual maturity. The differences in slopes between many of these individual trajectories indicates that the growth rates can vary significantly between individuals and that these differences may be maintained over long time frames.

3.3.6.3.2 *Otolith based growth estimates*: To establish the length at age relationship for females of this species, 19 fish were collected over as wide a size range as possible in the Huon region in April 1993. Ages were determined from what appeared to be annual growth rings in sagittal otoliths, which were identical to those of the males of this species. The von Bertalanffy growth parameters  $L_\infty$ ,  $K$  and  $T_0$  were estimated from the age data and are given in Table 3.2. The von Bertalanffy curve derived from these estimates is shown fitted to the age length data in Fig. 3.35 ( $r^2 = 0.78$ ). The value estimated for  $L_\infty$  (29.1 cm) was similar to that estimated from the tagging data



(27.3 cm). The maximum age determined from otolith ages females of this species was 7.5 years, and was found in fish from the East Coast collection (Fig 6.5).

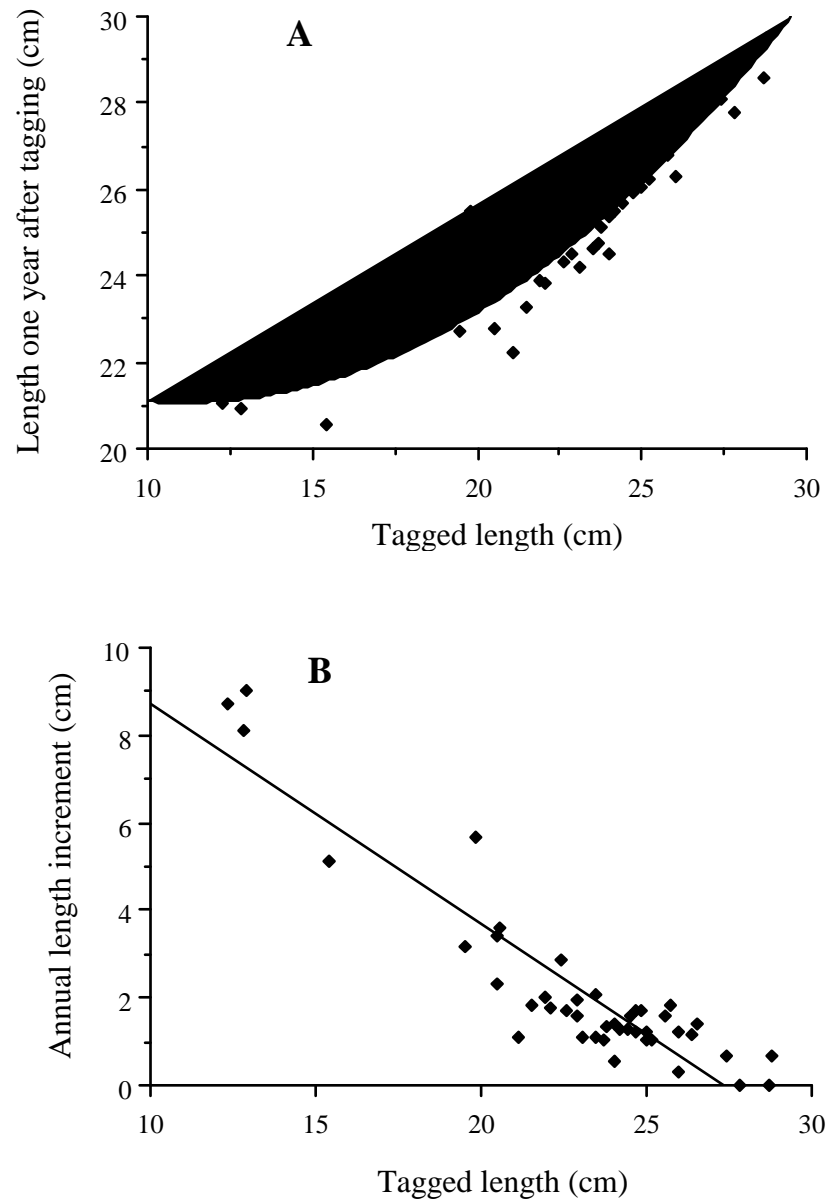


Figure 3.32 Annual growth data from 42 *Meuschenia australis* females tagged and recaptured at Arch Rock, Tasmania, between May 1990 and January 1994. Presented as (A), a Ford-Walford plot of length at tagging against length one year after tagging (fitted with a 2nd order polynomial), and as (B), a Manzer-Taylor plot of annual length increment against tagged length.

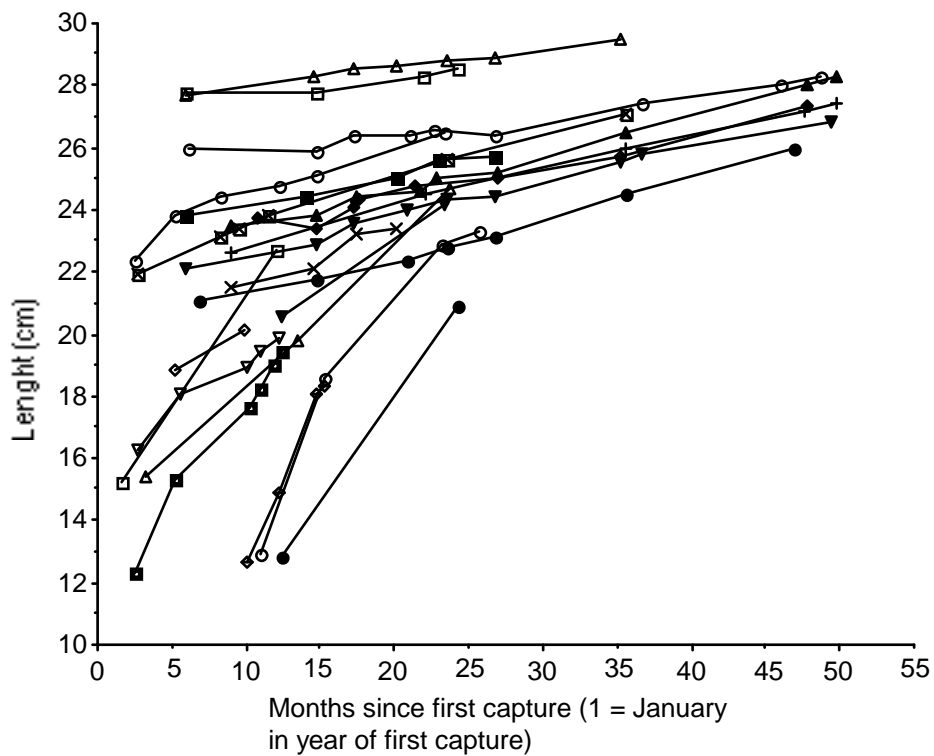


Figure 3.33 Growth trajectories of a selection of *Meuschenia australis* females tagged at Arch Rock. Trajectories are based on recaptures between May 1990 and January 1994.

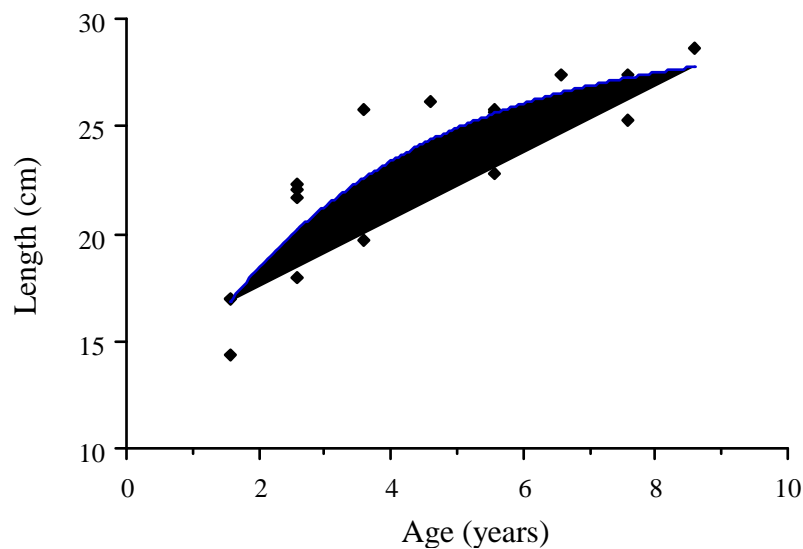


Figure 3.34 *Meuschenia australis* female length at age relationship, for fish collected in the Huon region survey (April 1993) and aged from counts of otolith annuli. The von Bertalanffy growth curve is fitted. Age estimates are based on the assumption of a September 1 birthdate.

3.3.6.3.3 *Validation*: As was discussed with respect to males, no new recruits were found until juveniles with lengths greater than 12 cm appeared. With the females, individuals in the 12-13 cm size range were recorded between October and March, and were assumed to all have been spawned in the previous year. By April 1991, a 12.3 cm individual tagged in October 1990 had grown to 18.5 cm, giving an approximate size range of the assumed 1+ cohort in April 1991 of 13-18.5 cm. This variability in length at year 1+, is probably attributable to the timing of spawning in this species, where individuals spawned early in September would have a four month growth advantage over those spawned in late December.

The three individuals from the Huon collection determined from otolith ageing to be in the 1+ cohort, all fell within the size range predicted from observations and tag recaptures, indicating that counting otolith growth increments may be a valid method of ageing young females of this species. To assess the validity of the estimated age relationship based on two or more growth rings, the von Bertalanffy estimate of length of the 1+ cohort from Fig. 3.35 was used to predict the mean lengths of ages 2+ and onwards using the tag based growth relationship of Fig. 3.32A. The resulting growth curve was compared with three possible von Bertalanffy curves derived from the otolith based growth. The best fit was to the curve assuming one growth annuli in otoliths per year, suggesting it was the most appropriate of the three possibilities. While the two curves (tag and otolith based growth) were not identical, they were similar enough to suggest, in a similar manner to the males of this species, that counting otolith growth rings is a valid and reliable method of ageing females of this species.

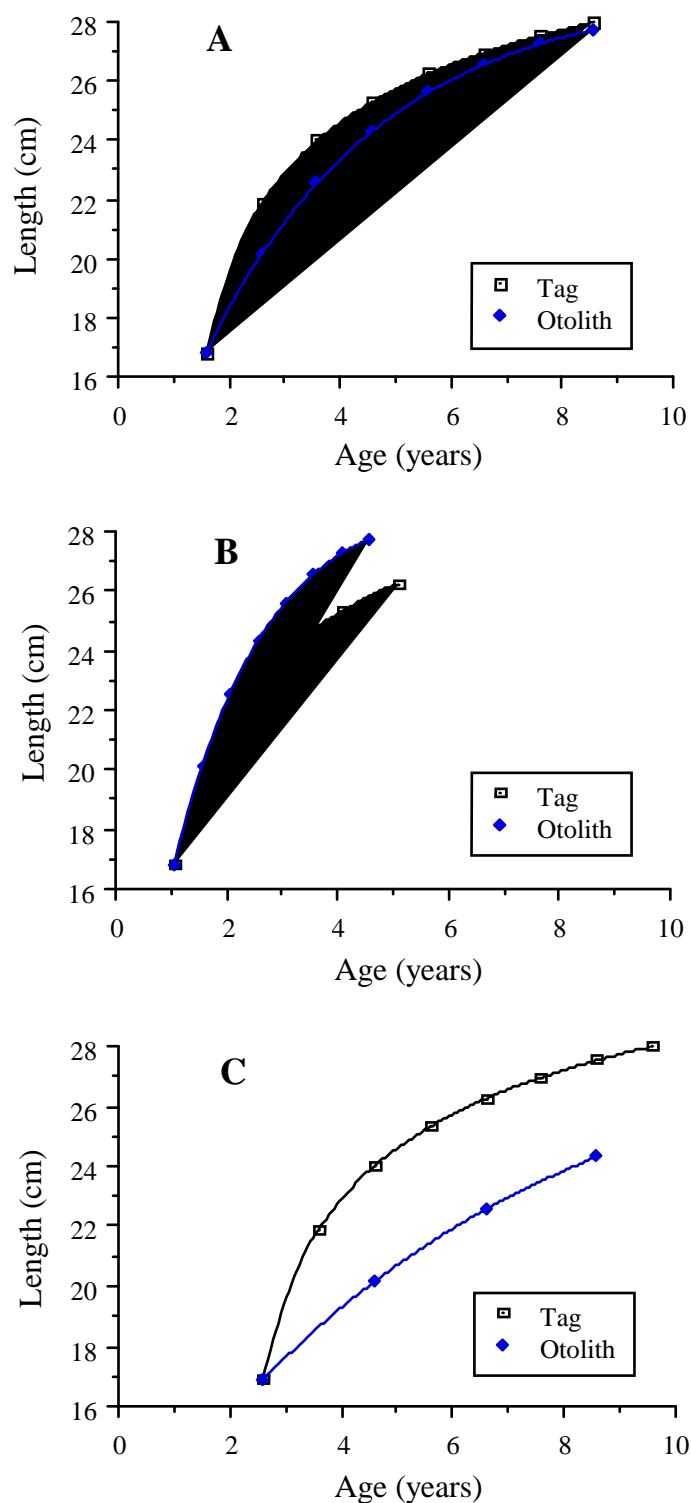


Figure 3.35 Comparison of the growth curve of *Meuschenia australis* females tagged at Arch Rock, with the von Bertalanffy curves derived from fish collected in the Huon region survey (April 1993) and aged from otolith annuli under three assumptions, (A) annuli are annual, (B) produced twice yearly, (C) produced once every two years.

### 3.4 Discussion

#### 3.4.1 Validation

A combination of mark-recapture growth estimation and visual observations of early year class size structure validate the length at age relationships determined from the counting of growth rings in otoliths for the six species in this study. This validation process would have been substantially improved however, if a large number of fish had been marked by oxytetracycline, or a similar marker, at the start of the study, and otoliths collected for sectioning at the conclusion of the study. The current view in the literature is that this is the only method of reliably validating the use of other ageing techniques (Francis 1992). Unfortunately insufficient resources were available for a study of this magnitude, and harvesting of marked fish would have interfered with the long term movement study being conducted on the same population.

The methods adopted in this study, (comparison of tagging data with age-length data) appear to be the second best option for validation. The main weakness of this method is that the growth parameters derived from the two different data sets are not directly comparable (Francis 1988a). This appears to be especially a problem when von Bertalanffy type growth parameters are required and the von Bertalanffy equation is transformed to  $\Delta L = (L_{\infty} - L)(1 - e^{-K\Delta t})$  (derived in Fabens 1965). Here, the  $\Delta L$  derived from age-length data is the expected annual increment, whereas the  $\Delta L$  from tagging data is a measured value, and the two are completely different parameters. A statistical comparison of the growth parameters derived from the two methods may therefore be invalid.

In a large scale study of the growth of western rock lobsters, *Panulirus cygnus*, Maller and DeBoer (1988) found large biases and inconsistencies in fitting the von Bertalanffy curve to recapture data when using either the simple model of Fabens (1965) or that of Sainsbury (1980) which assumes each animal has its own  $L_{\infty}$  and  $K$ . They decided that

such estimates are unreliable. For this reason, the von Bertalanffy parameters derived from age-length data in this study were not statistically compared with ones derived from the tagging data for the purposes of validation. Instead they were compared with curves derived from Ford-Walford plots using the method of Manzer and Taylor (1947), where an estimated length at age can be derived by extrapolating forward along the fitted line of the plot, from a "known" length at age. If a line of best fit is used on the Ford-Walford plot rather than a simple linear regression (except when this is appropriate), changes in  $K$  (the growth constant) can be taken into account. Ricker (1975) recognised that  $K$  does not always remain constant and showed four different types of long term growth curves.

The curve comparisons made in this study all indicated that the growth rings visible in sagittal otoliths were produced annually. While curves derived from recaptures were not perfect fits to the von Bertalanffy curves derived from length at age estimates based on the assumption of one growth ring per year, they were still closer to this curve than to curves based on the assumptions of two rings per year or one every two years.

Perfect fits between the two types of growth curves were not expected because of their different origins, and in general most tagging based curves were found to under-estimate growth initially, and then to over-estimate growth as  $L_{\infty}$  of the von Bertalanffy curve was approached. It is likely that these differences are due to two main effects. Firstly, growth of tagged fish may be slower than untagged fish due to various factors such as increased drag, and sores and infection at the tag entry site. McFarlane and Beamish (1990) demonstrated that external tags effect the growth of female sablefish (*Anoplooma fimbria*) by slowing growth by approximately 40% between the year classes 2+ and 4+ and an average of 25% between the year classes 2+ and 9+. Males of this species were not as significantly effected by tagging. While the impact of tagging on growth will depend upon the species and type of tag, it is apparent that this impact can

be significant and should be taken into account when tag-based growth is used for validation and to draw inferences about growth in the untagged population.

The second effect of tag based growth estimation appears to be related to over-estimation of the growth rate of the untagged population as it approaches  $L_{\infty}$ . This effect appears to be related to an inherent bias of tag-based growth, caused by intra-specific variation in growth rate and  $L_{\infty}$ . As size increases, the proportion of slower growing fish in the population decreases, as, at any particular length, they have lived longer and have therefore been subject to natural mortality and predation for longer. Therefore growth estimates become increasingly biased by the faster growing fish as size increases. This is compounded by individual differences in  $L_{\infty}$ , where slower growing individuals never reach the length achieved by those with faster growth. Under this assumption, the  $L_{\infty}$  of length based growth curves would therefore be expected to reflect that of the fastest growing individuals, rather than the population mean, which is the value usually derived from length at age data. These differences are evident if Tables 3.1 and 3.2 are compared, where the  $L_{\infty}$  of most species and sexes was greatest when estimated from tag-recapture data.

#### 3.4.2 *Individual growth variability*

For all species where sufficient tag recaptures were obtained to examine growth based on tagging, individual growth rates were highly variable. Substantial variation in individual growth rates of fishes has been widely reported in the literature, and ranges over several spatial scales, from differences between habitats (Sogard 1992, Victor and Brothers 1982) through differences between isolated but similar habitats (Pitcher 1992) to differences within the one location (Beckman *et al.* 1991, Pitcher 1992). While many of the differences in growth between habitats and locations may be explained in terms of variation in biological and physical parameters between sites, this is not usually the case at a single sampled location. Here, genetic and social factors have been suggested as the major cause of growth variability (Chevassus 1982) and have been shown to be important in controlled experiments on tench, *Tinca tinca*, by Backiel (1986).

At Arch Rock, the observed variability in length based growth is probably attributable to three main factors. The first of these is likely to be habitat variation, especially in *N. tetricus*, *P. psittaculus* and *P. laticlavus*, species in which individuals are either territorial or have very limited home ranges. This variation arises due to the shelter from prevailing westerly winds and southerly swells that the island provides along its eastern and northern coasts, thus providing a range of habitats from the exposed southern and western shores to the sheltered northern and eastern shores. This difference is directly reflected in the macroalgal communities which range from domination by *Ecklonia radiata* and *Durvillea potatorum* on the southern coast to *Sargassum fallax* and *Macrocystis pyrifera* on the northern coast. The effect of this habitat variation is likely to be less important for *N. fucicola* and *M. australis*, species in which the majority of individuals ranged over the entire reef on a daily basis and were therefore better able to overcome any localised resource limitation.

The second factor likely to influence growth is genetic variation in growth rate and  $L_{\infty}$ . This appears to be most obvious in female *M. australis*, where growth reaches a plateau after approximately two years. The length at which growth slows, varies greatly between individuals, and is probably genetically based, although it could also be related to the length at which sexual maturity is reached and energy is diverted from somatic growth to reproduction.

The third factor likely to influence growth is social interaction. This would appear to be particularly the case during the breeding season, which for all the species in this study, extended from at least early September to late December. During this time males were observed actively courting females, and in the case of territorial males, actively defending territories from intruding males. While conspecific levels of aggression were low between females of all species, females nevertheless expended much time avoiding males, especially in species such as *P. vittiger*, *M. australis* and *N. fucicola* where there



was a 1:1 sex ratio. Such social interactions obviously impacted on the time available for feeding, and would therefore at least potentially impact on growth, with any variation in the level of social interaction being reflected in growth rates.

This variability in individual growth rates for tag based growth was also reflected in the length at age relationships described from otolith ageing, as these relationships are not only influenced by individual growth rates, but also by the timing of recruitment. As all species in this study spawned over at least a four month period, the earliest spawned in each age class would be expected to have a significant growth advantage over the last spawned; this is approximately 4 cm in most species.

#### 3.4.3 Labrid growth

The growth and age structure of the labrids in this study falls within the range described for similar sized species of temperate labrids from New Zealand and Europe. At Leigh in north eastern New Zealand, *Notolabrus* (= *Pseudolabrus*) *celidotus* lives to 7 years and grows to 27 cm, while *Notolabrus* (= *Pseudolabrus*) *inscriptus* lives up to 20 years and grows to approximately 40 cm (Thompson 1981). In Europe *Crenilabrus melops* lives to nine years and grows to 24 cm, while *Labrus mixus* lives to 17 years and grows to 35 cm (Costello 1991).

*Notolabrus fucicola* is a species found in New Zealand as well as Tasmania. At Leigh in north eastern New Zealand it is reported to live to 15 years and grow to 34 cm (Thompson 1981). This compares with a maximum age of 17 years and maximum length of 39 cm found in this study for the Huon region of south eastern Tasmania. While *N. fucicola* is a secondary gonochoristic species (see Chapter 4) both sexes grow at the same rate, indicating that a similar amount of energy must be diverted into reproduction in both sexes.

The age and growth of *N. tetricus* has been previously described from South Australia in a brief study by Shepherd and Hobbs (1985) which examined the growth relationship from the scales of 58 speared fish. Their growth curve is similar to the one derived from this study, considering the habitat and temperature differences that must exist between the respective study sites. The mean size at maximum age from the South Australian study was 38 cm at eight years, compared with 31 cm at nine years in this study.

#### 3.4.4 *Monacanthid growth*

Very little is known about growth of monacanthid fishes. This, in part, arises from the fact that this is not a very speciose family, and it is not well represented in the tropics or New Zealand where much of the research effort on reef fishes has been concentrated. Estimates of maximum age reported for monacanthids include 10 years in *Navodon septentrionalis*, a species commercially exploited in the waters off China (Chien and Hu 1980) and 7 years in *Parika scaber*, a species found in New Zealand and south-eastern Australia (Thompson 1981). In the related family Balistidae, *Pseudobalistes fuscus* was estimated to live to 7 years, with differential growth between sexes, with females reaching 25-30 cm and males reaching 40-45 cm (Fricke 1980). Growth in *Parika scaber* in the marine reserve at Leigh, New Zealand, was described to be to 14 cm in the first year and to 26-29 cm in the second year, after which growth stopped (Thompson 1981). The growth of the two monacanthids in this study appears similar to that of *Parika scaber*, as growth is fast in the first 2-2.5 years, after which growth slows appreciably in both species. Growth is also similar to that reported for *Pseudobalistes fuscus*, in that females do not grow as fast as males, although in *P. vittiger* at least, the growth rate of the sexes appears similar in the first year.

In *M. australis* the estimated maximum ages of 8 years for females and 7 years for males, appear to be close to the average for this family, while that estimated for *P. vittiger* of 3+ years for males and 5+ for females is slightly below average, especially

when it is considered that the majority of males live no longer than 2.5 years and females 3.5 years.

The growth data presented for most species in this chapter deal with growth at Arch Rock and the Huon region because that is where the tagging work was carried out. As growth in this area may be atypical, due to the influence of the adjacent Huon River with its resulting impact on light regime, temperature, salinity and nutrient levels, the results of a survey on inter-population growth variation presented in Chapter 6 may better describe the average growth of most of the species included in this study.

## **Chapter 4 Reproduction**

### **4.1 Introduction**

#### *4.1.1 General:*

Growth is known to vary between the sexes in many fish species (Wootton 1990). For this reason any study examining growth should also include a study of the sexual system of each species investigated, so that the sex of individual fish can be reliably determined on the basis of simple features such as external coloration and gonad shape and colour, allowing potential sex related differences in growth to be examined. As sexual systems can often be complex, particularly in families such as the Labridae (Thresher 1984), an understanding of the sexual systems used in related species may be important in providing clues about the system used in the species under investigation.

#### *4.1.2 Labrid reproductive biology*

In the family Labridae, the majority, if not all, of the tropical species that have been studied are protogynous hermaphrodites, with most species displaying sexual dichromatism and generally having complex socio-sexual systems (Thresher 1984). These social systems, and a theoretical analysis of the fitness of each system, are discussed in detail by Warner and Robertson (1978).

In hermaphrodite species, the juvenile and female coloration is referred to as initial phase (IP) coloration, whilst that of the male derived from a sex change from a female is called the term phase (TP) coloration. The transition from female to male in most species is thought to be controlled predominantly by social conditions, where subordinate females are inhibited from changing sex by the presence of males, which are usually larger (Thresher 1984). In several species, experimental removal of the male has been shown to result in one of the larger females undergoing a rapid sex reversal to fill his role (Reinboth 1980).

While the majority of IP individuals in most species are females, in many tropical species a small proportion of fish with IP coloration (usually between 10-15%) are males. Species with both IP and TP males are referred to as diandric, and those with only TP males as monandric (Warner and Robertson 1978). Initial phase males in diandric species have the same coloration as IP females, allowing them to remain undetected in the territory of the larger and usually territorial TP males, where they may sneak fertilisations with the resident females. These IP males are usually, but not always, primary males. Primary males generally have solid gonads (e.g. *Labrus mixtus*, Dipper and Pullin 1979) whereas the secondary male gonad is either hollow, reflecting its origin as an ovary with a lumen (e.g. *Labrus bergylta*, Dipper and Pullin 1979), or is solid but surrounded by a membrane derived from the ovarian wall (e.g. *Thallasoma cupido*, Meyer 1977). Most TP males are of the secondary type, whilst most IP males are primary, however, in some species there are IP individuals which have changed sex prior to maturation, and therefore are secondary males with secondary gonads (e.g. *Notolabrus celidotus*, Jones 1980). Males of this type have been termed pre-maturational males by Warner and Robertson (1978).

In the Southern Hemisphere, the majority of temperate labrids investigated so far are protogynous hermaphrodites, e.g. *Notolabrus celidotus* (Jones 1980) and *Pseudolabrus miles*, *Notolabrus inscriptus*, *Pseudolabrus luculentus*, *Bodianus oxycephalus* and *Coris sandageri* (Thompson 1981). In *N. celidotus* and *C. sandageri*, a small proportion of IP individuals are pre-maturational secondary males (Thompson 1981).

In the Northern Hemisphere temperate labrids, there may be a greater proportion of gonochoristic species than in the Southern Hemisphere, as three of the five common European species are gonochorists (Costello 1991). Of the two protogynous species, one (*Labrus bergylta*), is monandric, while the other (*Labrus mixtus*) is diandric, with 12% of IP individuals in this species being males with primary testes (Dipper and Pullin 1979). Even within the gonochoristic species, some equivalents of IP males exist. In the

gonochoristic species *Crenilabrus melops*, Dipper and Pullin (1979) reported that about 20% of individuals with female secondary sexual characteristics were primary males. These were termed type 2 males by Dipper and Pullin (1979), and have been termed accessory males elsewhere (e.g. Costello 1991) as, unlike the type 1 males of this species, they do not hold territories or build nests.

Another unusual sexual system is found in the temperate labrid *Oxyjulis californica* in North America. In this system, termed secondary gonochorism, the sexes are genetically determined, with all males having secondary testes which have developed the male condition before maturation (Diener 1976).

In the species of tropical labrids in which spawning has been observed, pair spawning appears to be the most common spawning behaviour, with eggs being released into the water column for dispersal. Although group spawning has also been observed in some of these species, it occurs infrequently, and is thought to be related to spawning involving IP males (Thresher 1978). Benthic egg deposition has not been recorded in tropical species, however it appears to be a common feature of temperate labrids, with four of the five common European species producing benthic eggs which are guarded in nests (Costello 1991), a behaviour which does not appear to be related to the sexual system.

#### 4.1.3 *Monacanthid reproductive biology*

Unlike the labrids, the monacanthids have not been studied in any detail, but this family appears to be much simpler in the number of reproductive strategies used. Thresher (1984), in a review of the monacanthids and the closely related balistids (triggerfish), reported that in the few studies published to date, males tended to be larger than females, with many species being sexually dimorphic and dichromatic. Although studies have looked for evidence of hermaphroditism in two species, none has been found (Chiba, *et al.* 1976, Matsuura 1976).

Many species of balistids and monacanthids that have been studied are benthic spawners, including the tropical species *Alutera schoepfi* (Clarke 1950), *Odonus niger* and *Pseudobalistes fuscus* (Fricke 1980), and *Oxymonacanthus longirostris* (Barlow 1987), and the temperate species *Paramonacanthus japonicus* (Nakazono and Kawase 1993). In these species egg care is provided by one or both parents, and males are usually territorial while females are home ranging.

Some examples of pelagic spawning behaviour have been reported, although actual spawning was not observed, and there is the possibility the these interactions may only have been aggressive (Thresher 1984). Territorial males have been reported for the southern temperate monacanthid *Parika scaber*, although this species has pelagic eggs (Thompson 1981) suggesting that spawning is pelagic.

#### 4.1.4 *The Tasmanian species*

In this study it was necessary to examine the sexual system of each of the six species in which growth was being investigated, as no previous studies of their sexual systems have been reported. This lack of knowledge has led to some confusion in popular fish identification books and taxonomic texts, as to whether some of these species are protogynous hermaphrodites or gonochorists, and the relationship between colour pattern and sex. Much of this confusion has arisen because intermediate colour patterns often exist between those typical of males and of females. Intermediate color patterns led Edgar *et al.* (1982) to suggest that *Meuschenia australis* may be a sequential hermaphrodite, and Last *et al.* (1983) to suggest that a similar situation may exist in *Penicipelta vittiger*.

In *Notolabrus fucicola* the ground coloration is highly variable, and tends to darken as fish age, suggesting a size related dichromatism. These characteristics appear to have led New Zealand authors to believe that protogynous hermaphroditism was usual in this species (Doak 1972, Thompson 1981). However, in a recent taxonomic review of this

genus, Russell (1988) reported that although coloration in *N. fucicola* was variable, there was no marked sexual dichromatism, and the sizes of males and females overlapped broadly. This observation tends to indicate that this species may not be hermaphroditic.

In the same review, Russell (1988) suggested that *Pseudolabrus psittaculus* was sexually monochromatic, having similar sized males and females; monochromatism was also reported by Last *et al.* (1983). Such observations would suggest that this species was gonochoristic. However, these observations differ from those of Edgar *et al.* (1982), who reported size related sexual dichromatism in this species, with females generally being smaller than males, an observation indicating that this species may actually be a protogynous hermaphrodite. Fortunately, the situation appears to be less confusing for *Pictilabrus laticlavius* and *Notolabrus tetricus* as there is general agreement in the literature that they are both sexually dichromatic, and that *N. tetricus* is a protogynous hermaphrodite (Last *et al.* 1983).

#### 4.1.5 Aim:

The specific aim of the study reported in this chapter then, was to clearly define the sexual systems of *Notolabrus tetricus*, *Notolabrus fucicola*, *Pictilabrus laticlavius*, *Pseudolabrus psittaculus*, *Penicipelta vittiger*, and *Meuschenia australis*, including the proportion of any IP males which may be mistaken for females, and the relationship between sex, size and colour pattern.

## 4.2 Materials and methods

### 4.2.1 Collection sites and methods:

Fish were collected at a number of locations and times during this study (Table 4.1), primarily because not all sites yielded enough individuals for proper analysis, but also because collections made after the end of the labrid breeding season contained many specimens with gonads too small to sex or dissect, and, for the hermaphrodite species,



large numbers were needed to be collected from several sites to examine geographic variability in the length at sex change. The site locations of the collections are shown in Fig 2.1 (Ninepin Pt, and Huon collections), Fig. 4.1 (Tinderbox collection), and Fig. 6.1 (East Coast collection).

Table 4.1. Details of collections made for investigation of the sexual systems of *N. tetricus*, *N. fucicola*, *P. laticlavus*, *P. psittaculus*, *P. vittiger*, and *M. australis*, between September 1990 and March 1994.

Collection	Date	Species collected	Sites
Ninepin Point	Sept. 1990	<i>N. tetricus</i> , <i>N. fucicola</i>	Ninepin Pt
Huon	April/May 1993	All	Arch Rock, Butts Reef Charlotte Cove, Roaring Beach
Tinderbox	Aug/Sept. 1993	All	Piersons Pt, One Tree Pt
East Coast	Feb/March 1994	All	Fortescue Bay Garden Pt Marion Bay, Spring Beach Stinking Bay

The capture methods employed included gill nets (with a range of mesh sizes), fish traps, spearing, and handlining. This range of methods was necessary to collect samples of each species over as wide a range of sizes as possible. Upon capture, fish lengths were measured to the nearest mm (total length) and their apparent sex from external coloration and morphology was recorded. They were kept on ice until returned to the laboratory, with the time between collection and subsequent analysis varying between 3 and 24 h.

#### 4.2.2 Analysis:

Upon return to the laboratory, fish were weighed to the nearest gram and their gonads were removed, weighed to 0.1 g, and their apparent sex recorded. The gonads were fixed and stored in 10% neutral buffered saline formalin until ready for processing. The fixed gonads were dehydrated in ethanol and then cleared in toluene before being embedded in paraplast by an automatic processor. Transverse sections were cut from several positions, where possible, along the length of the embedded gonad at 7 µm

thickness. Once cleared, the sections were stained with eosin and haematoxylin. The stained sections were then examined for any evidence of sex inversion, and to determine whether testes were of primary or secondary origin. More gonads were sectioned from the labrids than the monacanthids, as the labrids have more complex reproductive systems.

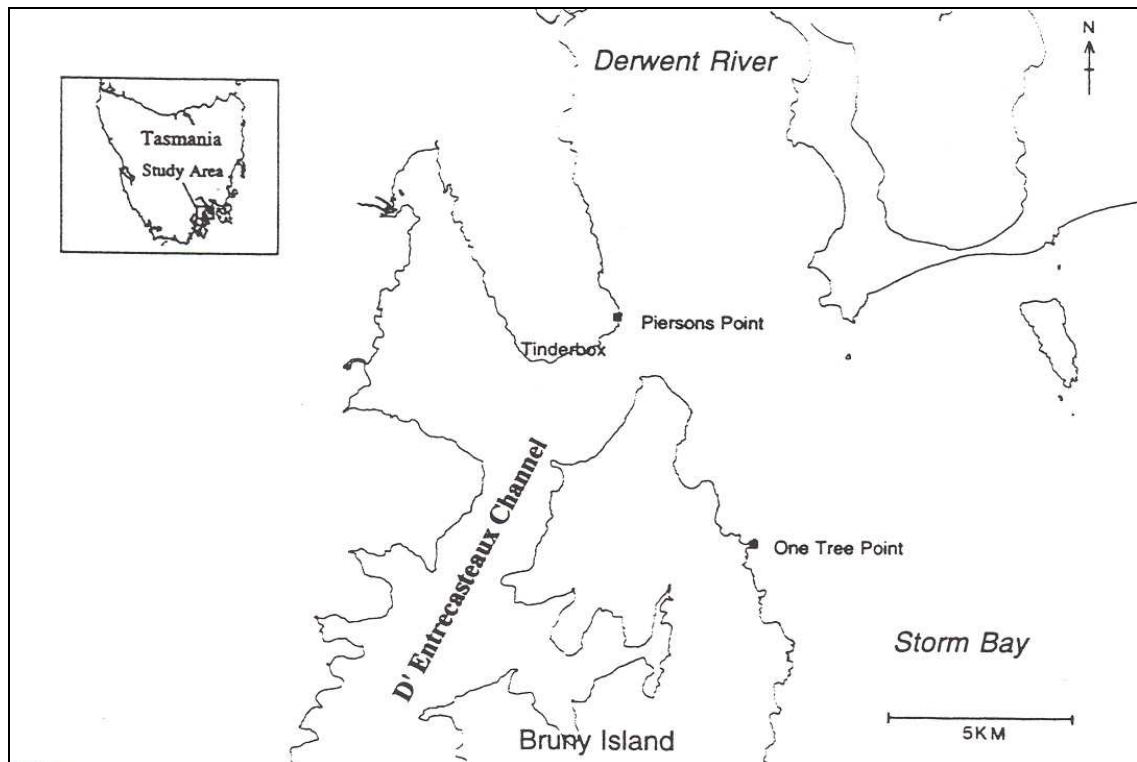


Figure 4.2 Sites at which the Tinderbox fish collections were made in August and September 1993

A large sample size was needed in the species shown to be protogynous hermaphrodites (*N. tetricus*, *P. laticlavius*, and *P. psittaculus*), in order to search for evidence of transitional gonads, and also for primary or secondary IP males which, if present, may have been rare. A large sample size was also needed for *N. fucicola*, to determine if any sex inversion was occurring after maturation. Once a sufficient number of sections had been examined in a particular species to determine the sexual system used, and the characteristic features of each gonad type were determined, the remaining gonads were simply examined under a light microscope, while fresh, to determine their sex. Ovaries removed from some *N. tetricus* and *N. fucicola* individuals collected in the breeding

season ( $n = 5$ ) were also examined for evidence of sequential spawning, by determining the size distribution of oocytes from histology sections.

In *P. laticlavius* and *P. psittaculus* the capture results from the capture, mark, and recapture experiment at Arch Rock were used to examine the relationship between length and sex, based on external coloration and morphology. These results are based on captures between June 1990 and January 1994; further details are given in Chapter 3.

While making behavioural observations on each species for the short-term movement study discussed in Chapter 2, some observations on reproductive behaviour were also made, including courtship and spawning; the detailed methods are given in Chapter 2). These observations were made during over 200 h of diving, with dives made randomly throughout the year, and effort being divided evenly between the species.

#### **4.3 Results.**

##### *4.3.1 Notolabrus tetricus*

*4.3.1.1 Sexual system:* A total of 448 individuals were collected and sexed from the four surveys (Ninepin Point, Huon region, Tinderbox, and East Coast). Of these, 112 were sexed from histologically prepared sections. No primary males were found, indicating that this is a monandric species. However, in the first survey at Ninepin Point, three fish resembling IP secondary males were found (Fig. 4.2), representing 10% of the IP fish collected from that site. These ranged in size from 24.5 to 24.9 cm, with the smallest TP male coloured fish being 27.7 cm in length. No IP males were found in subsequent surveys in the Huon region (Fig. 4.3) or at the East Coast sites (Fig. 4.4). Where small functional males were present, all were of a length which was within the size range that the IP to TP colour transition occurs, and appear to be part of the normal transition process where gonad sex inversion precedes colour change. If pre-maturational secondary males were present in this species, they should have been represented in all IP size classes, but this was not the case.

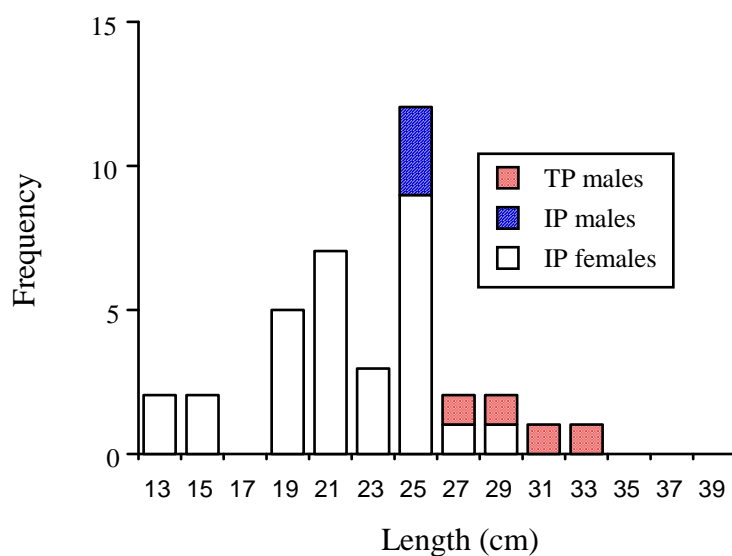


Figure 4.2 Frequency histogram showing the relationship between length, sex and colour phase in *Notolabrus tetricus* collected at Ninepin Point, Tasmania, in September 1990. All fish were sexed by examination of fresh gonads.

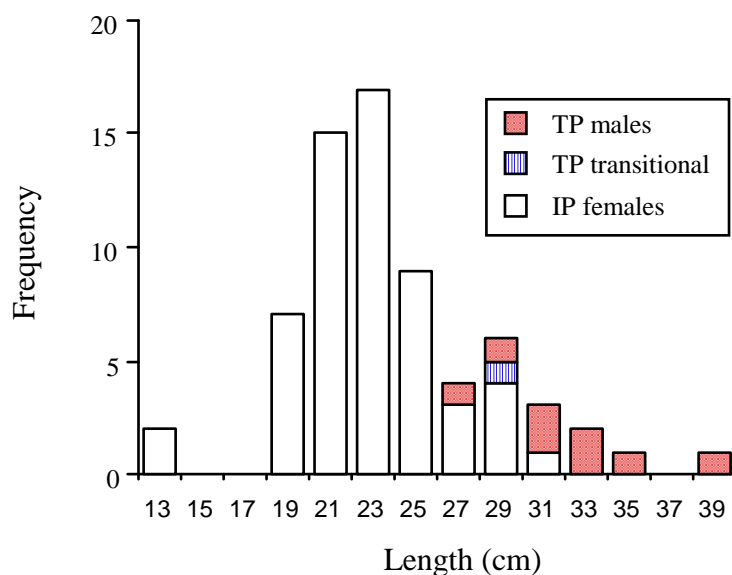


Figure 4.3 Frequency histogram showing the relationship between length, sex and colour phase in *Notolabrus tetricus* collected at sites in the Huon region survey, in the vicinity of Huon Is., Tasmania, in April 1993. All fish were sexed by histological examination of gonads.

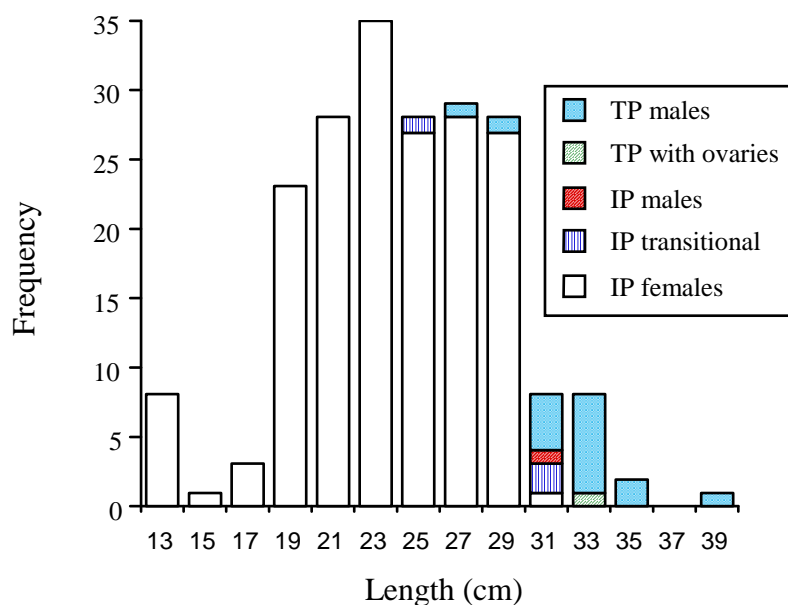


Figure 4.4 Frequency histogram showing the relationship between length, sex and colour phase in *Notolabrus tetricus* collected at sites in the East Coast survey in February 1994. Fish less than 27 cm were sexed from colour phase and microscopic examination of fresh gonads. Fish greater than 27 cm were sexed by histological examination of gonads.

One individual was found with male coloration and functional ovaries (Fig. 4.4) indicating that the sexual transition did not always involve gonads inverting first. In this species the sexual transition usually occurred over a fairly narrow size range, with most transitions happening between 27 and 32 cm, and the size at transition appeared similar at all the locations surveyed (Figs 4.2-4.4) although analysis of this was limited by difficulties in capturing enough of the less abundant and more evasive larger individuals. The age of sexual transition ranged from 6+ to 9+ in the Huon survey, and 5+ to 7+ in the East Coast survey, with the earlier sex change at the East Coast sites possibly being due to the faster growth recorded there. (Details of growth differences between the Huon region and the East Coast sites are given in Chapter 6).

4.3.1.2 *Histology*: All stages in the transition from ovary to testis were found in the histologically prepared gonad sections. Ovaries were found in most IP fish, and a typical

ovary with eggs in several stages of vitellogenesis is shown in Fig. 4.5a. Transitional gonads were occasionally found in the largest IP fish, and a typical transitional gonad with atretic oocytes and packets of spermatocytes and spermatids is shown in Fig. 4.5b. Testes were found in all but one TP fish, and the typical testes structure, with the large lumen characteristic of secondary development, is shown in Fig. 4.5c. No transitional gonads were found in fish collected in August and September, near the start of the breeding season, even though a large number of gonads were examined ( $n = 48$ ), whereas four of this type were found from 64 gonads collected between February and May, suggesting that sex change may be delayed during the spawning season.

Females collected in August generally had ovaries with eggs in several stages of vitellogenesis (Fig. 4.5a) and several size classes (Table 4.2) and included some post-ovulatory follicles which were filling in with granulosa cells. The range of egg sizes, in combination with the post ovulatory follicles (which, when present, indicate that

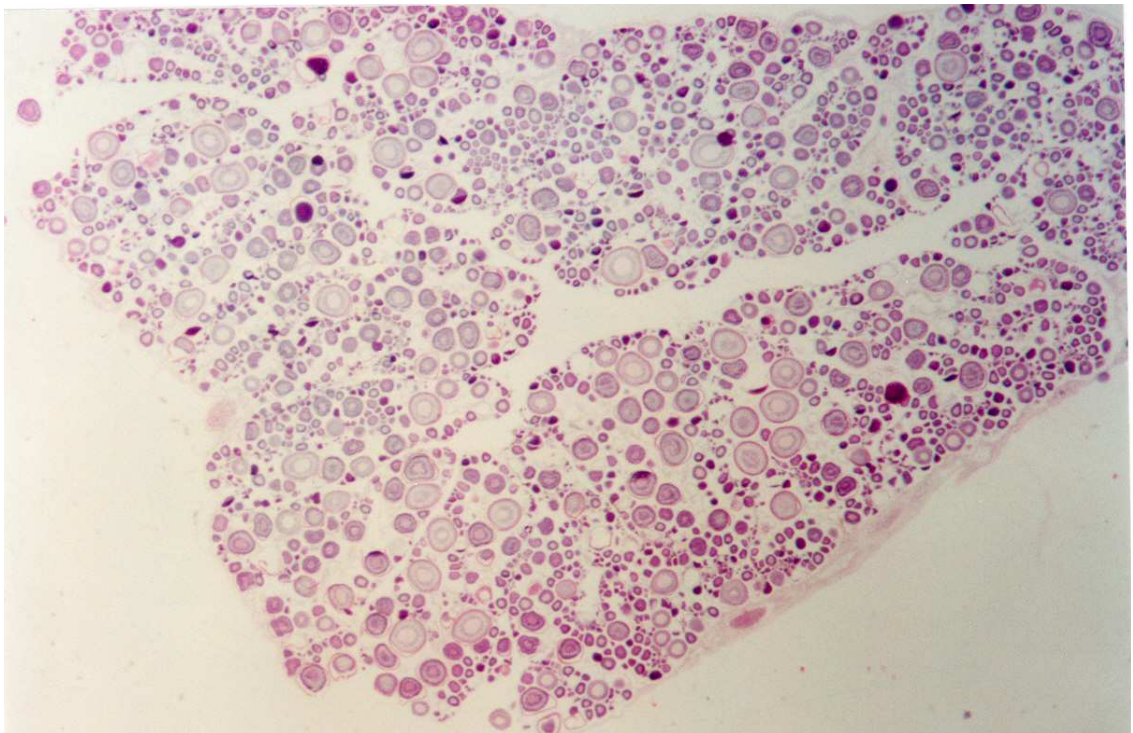


Figure 4.5a Low power TS of an ovary of a *Notolabrus tetricus* female collected in August 1993. Note the range of oocyte diameters, which indicates that this species is probably a sequential spawner. Scale 1 cm = 500  $\mu$ m.



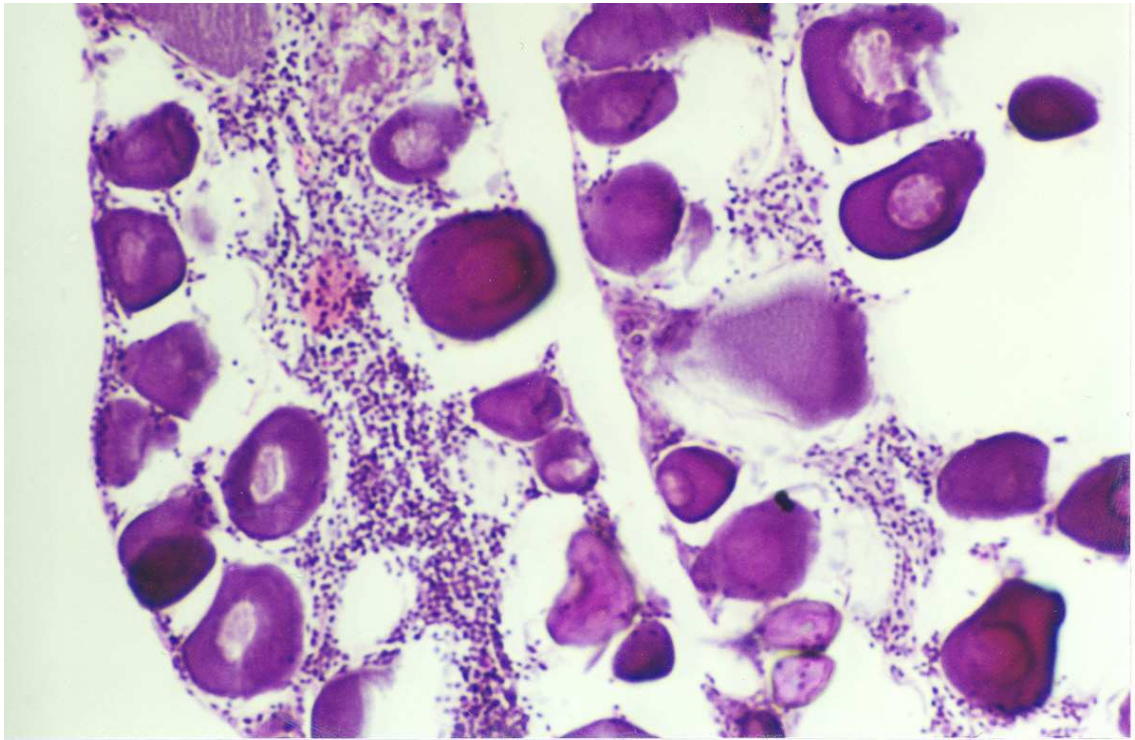


Figure 4.5b High power TS of a gonad of a *Notolabrus tetricus* individual undergoing sex inversion. Note the dense clusters of spermatocytes distributed amongst the residual oocytes. Scale 1 cm = 33  $\mu$ m.

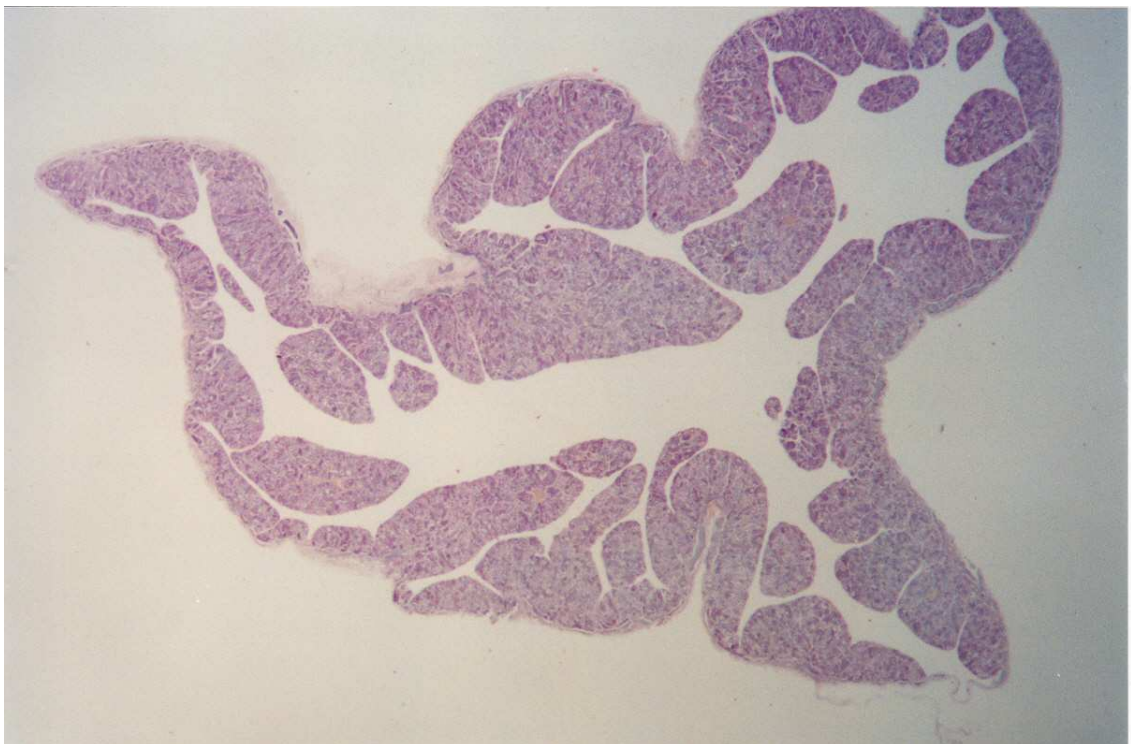


Figure 4.5c Low power TS of a testis of a *Notolabrus tetricus* male collected in August 1993. Note the distinct remnant ovarian lumen, a characteristic feature of secondary males. Scale 1 cm = 500  $\mu$ m.

Table 4.2 Mean and (standard deviation) of percentage occurrence of oocytes by size class in ovaries of *Notolabrus tetricus* and *N. fucicola*, collected at Tinderbox, Tasmania, in August 1993. Two hundred oocytes were counted in each ovary.

Oocyte dia.	<i>N. tetricus</i> (n=5)	<i>N. fucicola</i> (n=5)
0-50µm	45.4 (6.8)	45.4 (3.7)
50-100µm	37.4 (5.8)	39.0 (6.4)
100-150µm	11.1 (2.6)	9.7 (3.1)
150-200µm	5.5 (4.4)	5.5 (4.4)
200-250µm	1.7 (1.1)	1.0 (1.5)
>250µm	0.6 (0.6)	

spawning had occurred at least once already) suggested that individuals of this species probably spawn a number of times over the extended breeding season. However, a more thorough collection made over the whole breeding season is needed to properly document this.

4.3.1.3 *Spawning duration*: The presence of post-ovulatory follicles in the ovaries of some fish collected in mid-August indicated that spawning had already commenced by this time. Oocytes in any stage of vitellogenesis were rare in fish collected in February, indicating that spawning had ceased. As some fish handled at Arch Rock in mid-January extruded eggs, it can be deduced that the spawning season in this species extends from at least mid-August to mid-late January, although a more detailed study of changes in GSI and oocyte condition is needed to confirm this.

4.3.1.4 *Reproductive behaviour*: Males of this species are territorial, while females are home-ranging, with ranges overlapping those of numerous females and two or three males (Chapter 2). Between August and January, males actively courted females, suggesting that this was the duration of the spawning season. The males display consists of spreading and raising the caudal fin while swimming in an arc around the female. While many hours were spent observing courting males, spawning was never observed.



Spawning is presumably pelagic, as no evidence of nest building or other behaviour associated with demersal spawning was ever observed.

#### 4.3.2 *Notolabrus fucicola*.

4.3.2.1 *Sexual system*: A total of 233 individuals of this species were collected over four surveys (Ninepin Point, Huon region, Tinderbox, and East Coast) of which 146 were sexed by light microscopy of fresh tissue, with 92 of these being further prepared for histological examination. The sex ratio was not significantly different from unity ( $\chi^2=0.014$ ,  $p = 0.91$ ) with 72 males and 74 females, indicating that this was almost certainly a gonochoristic species. It was unusual however, in that unlike most gonochoristic species, the male gonads were secondary in origin rather than primary. The testes of all the males examined clearly had a residual lumen, although it was difficult to recognise initially, as the testes had split and evaginated in all mature specimens (Fig. 4.6b).

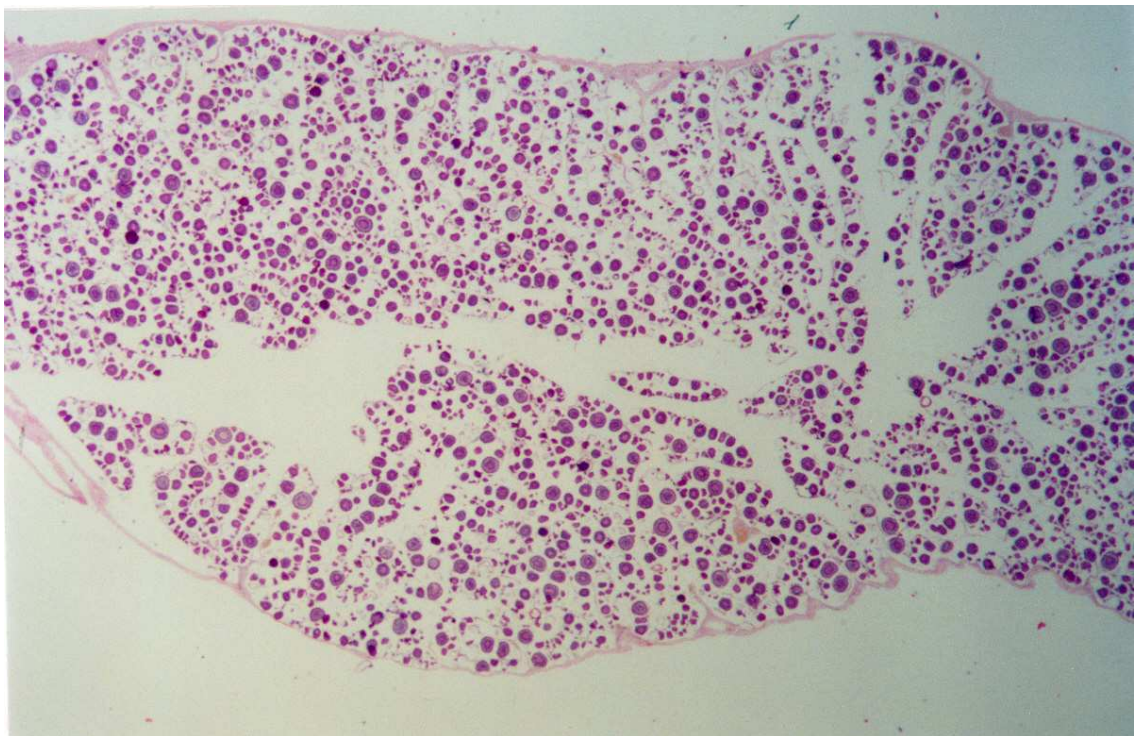


Figure 4.6a Low power TS of an ovary of a mature *Notolabrus fucicola* female, collected in August 1993. Note the range of oocyte diameters, indicating that this species is probably a sequential spawner. Scale 1 cm = 300  $\mu$ m.

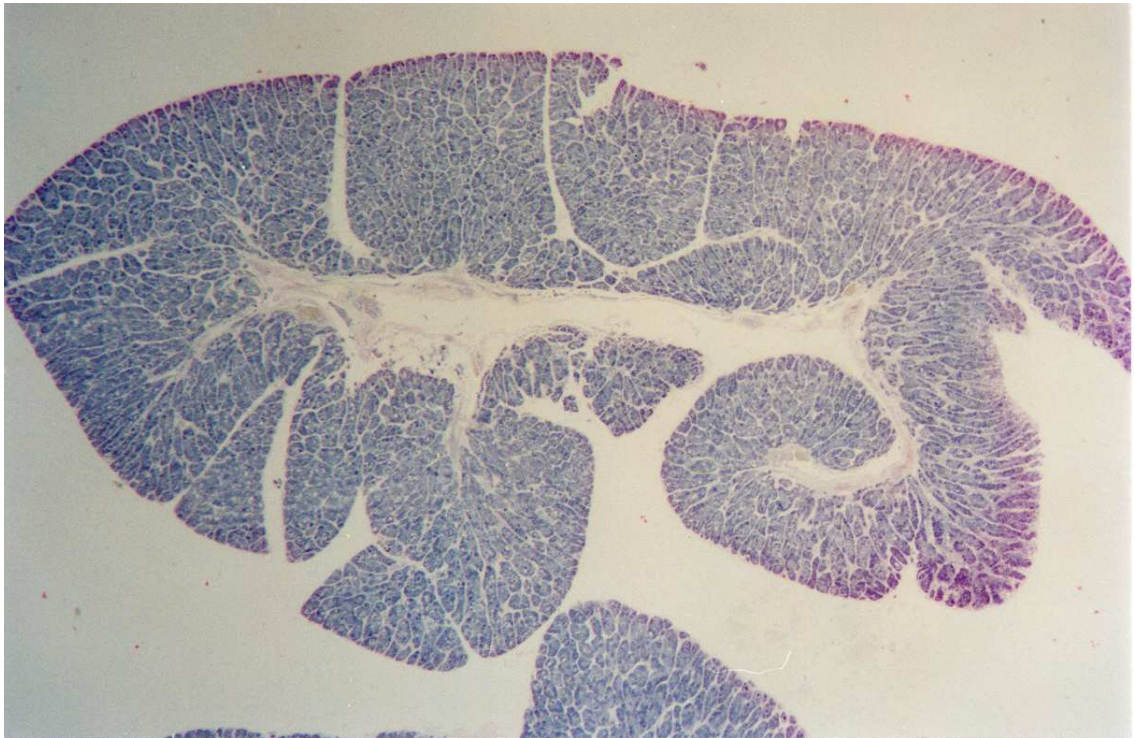


Figure 4.6b Low power TS of a testis of a *Notolabrus fucicola* male, collected in August 1993. Note how the testis has split and evaginated. If it had not split, this testis would have had a large central lumen, a characteristic feature typical of secondarily derived males. Scale 1 cm = 600  $\mu$ m.

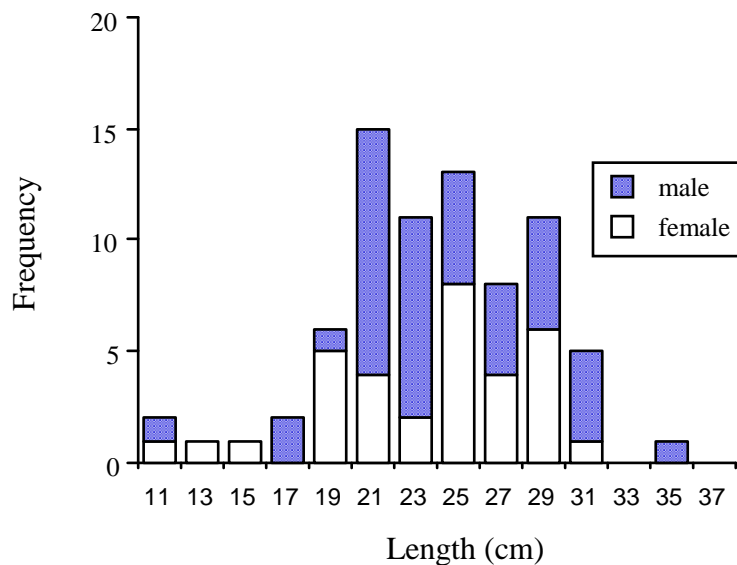


Figure 4.7 Frequency histogram showing the distribution of length by sex in *Notolabrus fucicola* collected at Ninepin Point in September 1990, and in the Huon region collection in April 1993.

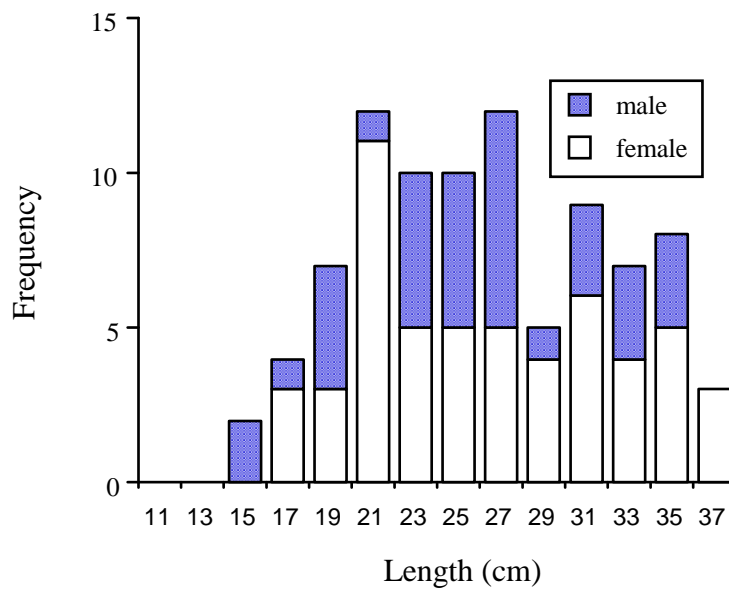


Figure 4.8 Frequency histogram showing the distribution of length by sex in *Notolabrus fucicola* collected from the East Coast sites in February 1994.

In the sex related frequency distributions of two population samples of this species (Fig's 4.7 and 4.8) there is a relatively even distribution of sexes throughout the size range indicating little evidence for sex inversion in larger females. The distribution by sex, between two size classes, large (>25 cm) and small ( $\leq 25$  cm), of these population samples, is shown in Table 4.3. When this distribution was examined by  $\chi^2$  analysis, no evidence was found against the null hypothesis that length distribution was independent of sex ( $\chi^2 = 0.97$ ,  $p = 0.32$ ).

Table 4.3. Distribution by sex and length, of all individuals of *N. fucicola* for which sex was determined.

Sex	Size Class	
	Small ( $\leq 25$ cm)	Large (>25 cm)
Male	29	43
Female	24	50

4.3.2.2 *Histology*: Fig. 4.6 shows the typical gonad structures found in this species, and includes an ovary with oocytes in several stages of vitellogenesis (Fig. 4.6a), and a mature male gonad which characteristically has ruptured and evaginated (Fig 4.6b). Females collected in August generally had ovaries with eggs in several stages of vitellogenesis (Fig. 4.6a) and several size classes (Table 4.2), with some individuals having post-ovulatory follicles filling in with granulosa cells. The variety of egg size classes (Table 4.2), in combination with the post ovulatory follicles (which, when present, indicate that spawning had occurred at least once already) suggests that individuals of this species may spawn more than once during the breeding season.

4.3.2.3 *Spawning duration*: The duration of spawning in *N. fucicola* was very similar to that described for *N. tetricus*. Post-ovulatory follicles were found in the ovaries of some fish collected in mid-August, while oocytes in any stage of vitellogenesis were rare in fish collected in February. As some fish handled at Arch Rock in mid-January extruded eggs, it can be deduced that the spawning season in this species extends from at least mid-August to mid-late January, although as with *N. tetricus*, a more detailed study of changes in GSI and oocyte condition is needed to confirm this.

4.3.2.4 *Reproductive behaviour*: Both sexes of this species are home-ranging, and display no evidence of territorial behaviour (Chapter 2). Many individuals range over the whole reef on a daily basis, with their ranges obviously overlapping the ranges of numerous others. From August to January, males were observed displaying to females, and presumably this coincided with the duration of spawning. The display usually involved raising the dorsal and anal fins while circling the female. Females were usually followed until they were discarded for another female or until the male was involved in a chase with another male. While the interactions between males were aggressive, they were never related to territorial defence, only to the presence of a female. Spawning was never observed; it is presumed to be pelagic, as no evidence of nest building or other behaviour associated with demersal spawning was ever observed.

#### 4.3.3 *Pictilabrus laticlavius*

4.3.3.1 *Sexual system*: A total of only 83 individuals of this species were collected from three surveys (Huon region, Tinderbox, East Coast). The number collected was limited by the fact that individuals of approximately 16 cm or less were not able to be easily captured in traps or nets, and were sufficiently cryptic to avoid capture by spearing. Of the 83 fish collected, 50 were sexed from histological sections of the gonads, while a further 17 (all large males) were sexed from examination of fresh gonads. Seventeen IP females, 29 TP males and four transitional fish (three with male coloration and one with female coloration), were determined from the histological examination of gonads. The distribution of these sexual stages by length at the Huon region and East Coast sites are shown in Figs 4.9 and 4.10.

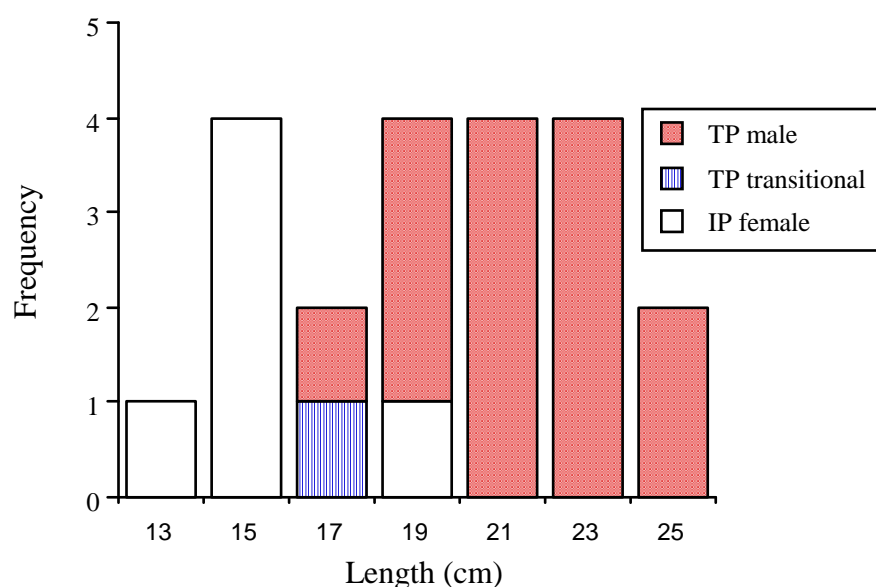


Figure 4.9 Frequency histogram of the *Pictilabrus laticlavius* sex/length relationship of fish collected in the Huon region in April 1994, based on histological examination of gonads.

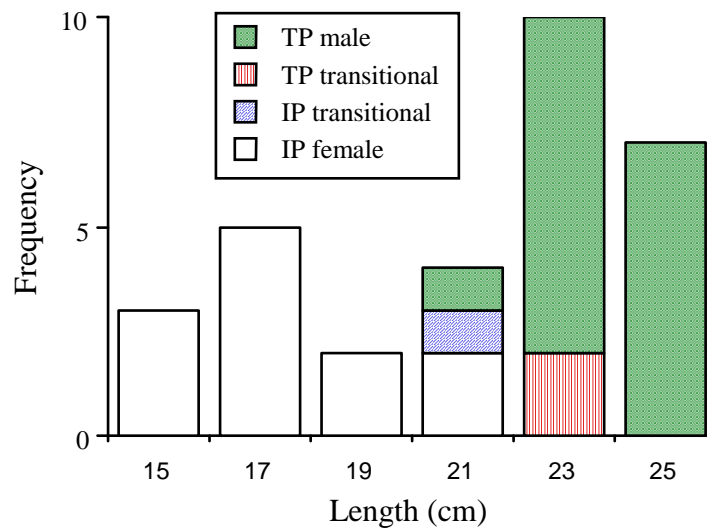


Figure 4.10 Frequency histogram of the *Pictilabrus laticlavius* sex/length relationship of fish collected in the East Coast survey, February 1994, based on histological examination of the gonads.

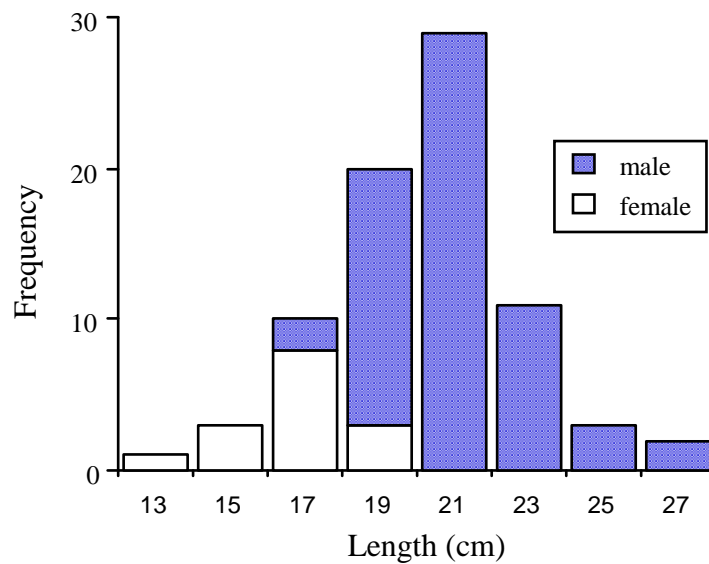


Figure 4.11 Frequency histogram of the *Pictilabrus laticlavius* sex/length relationship of fish captured in fish traps at Arch Rock, between September 1992 and January 1994, based on external coloration of fish.

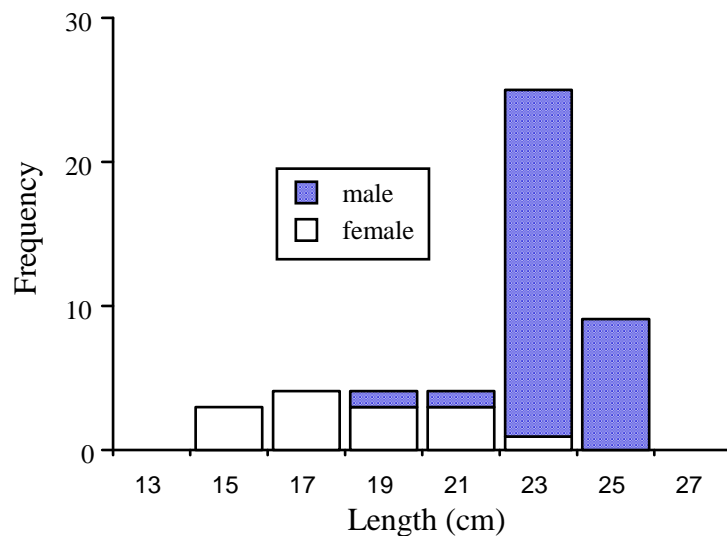


Figure 4.12 Frequency histogram of the *Pictilabrus laticlavius* sex/length relationship of fish collected in the East Coast survey, February 1994, based on external coloration of fish.

All males were secondary. A sufficiently large number of individuals ( $n = 67$ ) were examined to suggest that, if primary males exist in this species, they must only form a very small proportion of the population. Likewise, no IP pre-maturational secondary males were found, and although the IP sample was small ( $n = 17$ ) it was sufficient to indicate that IP secondary males, if present, are rare and would not make a substantial contribution to the sexual system of this species. The sexual system therefore appears to be monandric protogynous hermaphroditism, with no IP males.

Sexual dichromatism is very pronounced in this species and colour change was clearly associated with sex inversion (Figs 4.9 and 4.10), such that external coloration is a very good predictor of sex. This relationship was used to examine larger sample sizes from the Huon and East Coast surveys for differences in the size at sex change, without the need to dissect the gonads to determine the sex of each fish. Most individuals captured at the Arch Rock site change sex at lengths between 17.4 cm and 19.4 cm (Fig. 4.11), lengths which correspond to ages 3+ to 4+ in April. At the East Coast sites, sex change



occurred between 17.4 cm and 22.5 cm (Fig. 4.12), lengths which correspond to ages 3+ to 5+ in February. Sexual maturity was reached at 2+ at the latter sites.

4.3.3.2 *Histology*: All stages in the transition from ovary to testis were found in the histologically prepared gonad sections, and examples of the three main stages are shown in Fig. 4.13. An ovary collected in mid-August with eggs in several stages of vitellogenesis is shown in Fig. 4.13a. Transitional gonads were identified by the presence of atretic oocytes and developing packets of spermatocytes and spermatids (Fig. 4.13b). The final stage of the transition are mature testes (Fig 4.13c), and were identified as being secondarily derived by the presence of a large residual ovarian lumen, a feature characteristic of protogynous hermaphroditism.

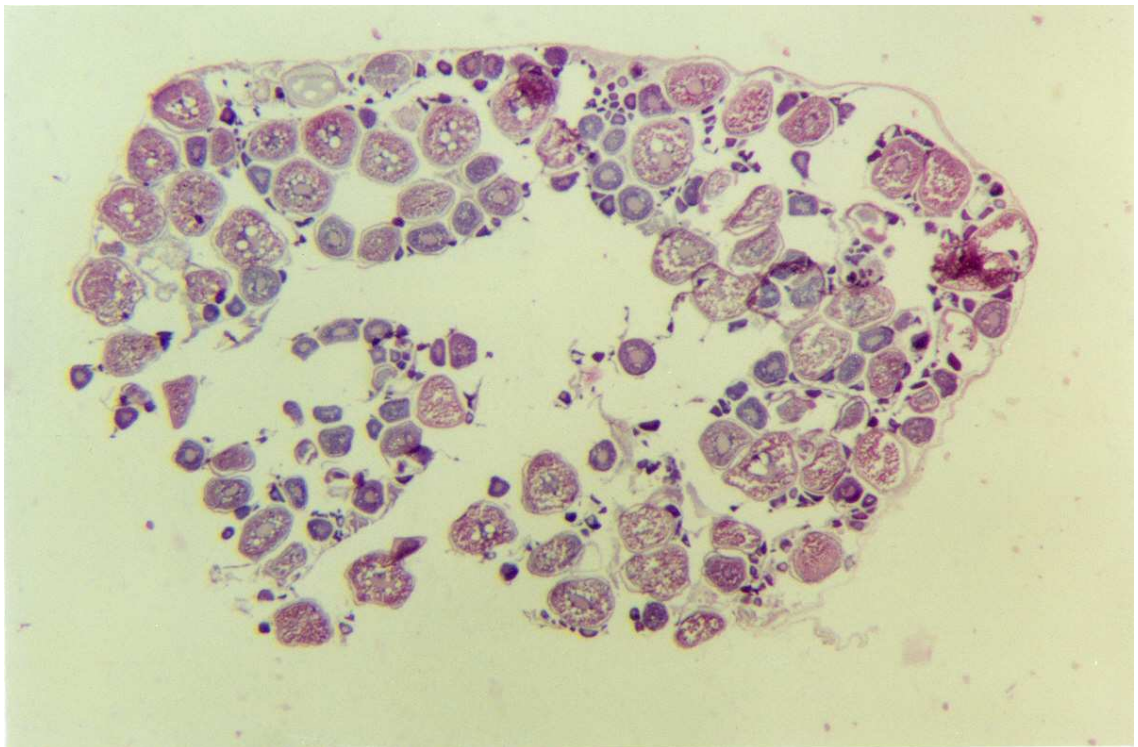


Figure 4.13a Low power TS of a ripe female *Pictilabrus laticlavius* ovary collected in August 1993. Note the range of oocyte diameters, indicating that this species probably spawns sequentially. Scale 1 cm = 500  $\mu$ m.



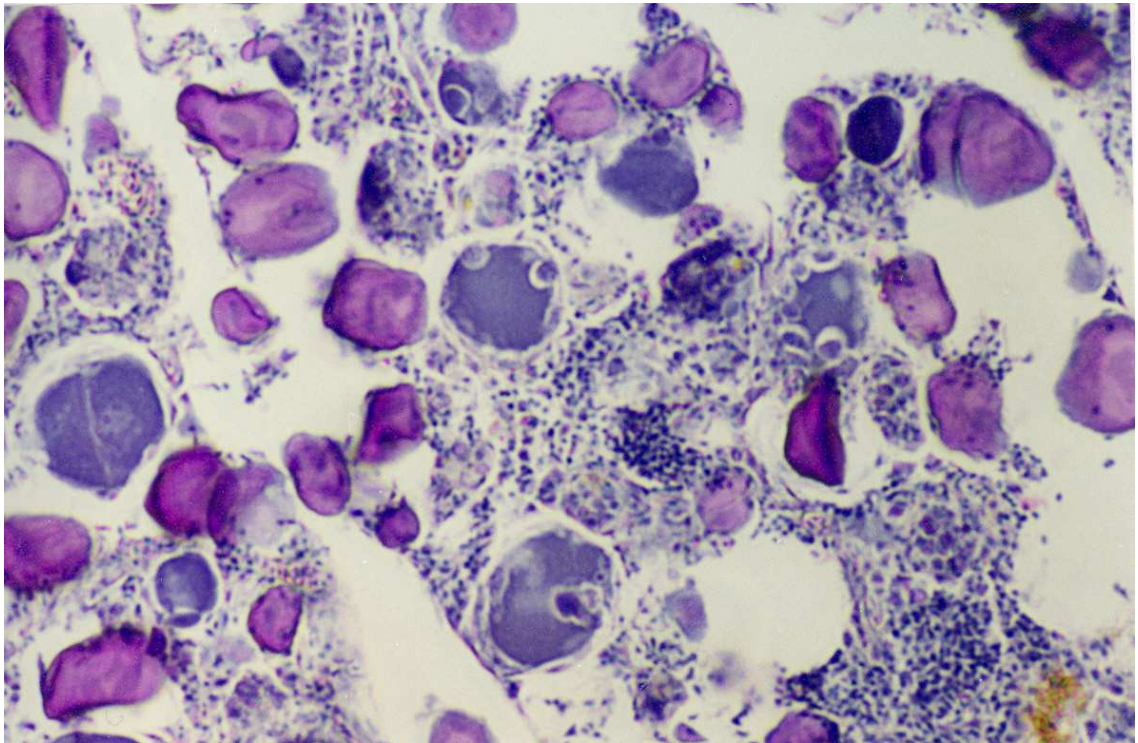


Figure 4.13b High power TS of the transitional gonad of a *Pictilabrus laticlavius* individual collected in February 1994. Note the dense clusters of spermatocytes distributed amongst the residual oocytes. Scale 1 cm = 33  $\mu$ m.

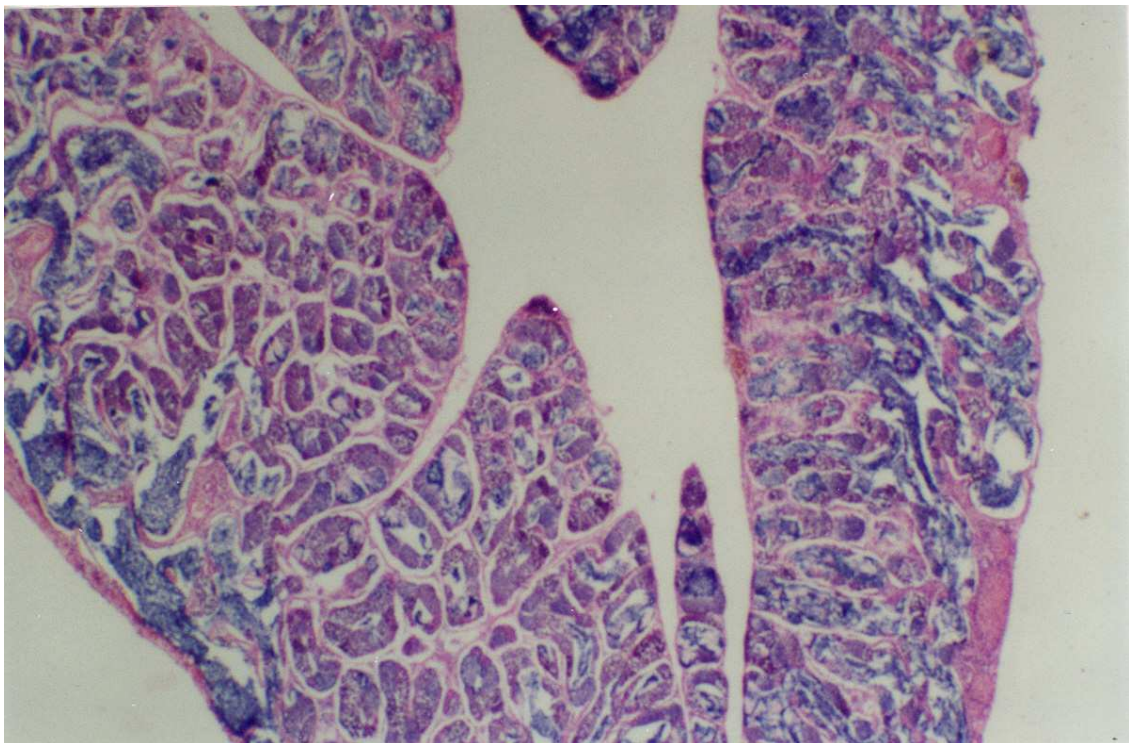


Figure 4.13c Low power TS of a mature male *Pictilabrus laticlavius* testes, collected in August 1993. Note the residual central lumen, a characteristic feature of sex inversion. Also note the secondary vas-deferens (top right) containing spermatozoa (stained dark blue). Scale 1 cm = 330  $\mu$ m.

4.3.3.3 *Reproductive behaviour*: Home ranges in this species are small, with males being territorial, at least during the spawning season (Chapter 2). Males were observed actively courting females from approximately mid-August to mid to late-January and, presumably, this courting behaviour coincided with the spawning period. The male courtship display consisted of raising the dorsal and anal fins while swimming past, and above, the female who was almost always hidden amongst algae. Pair spawning was observed once in this species, and was characterised by the pair rapidly swimming approximately 2 m vertically together, shedding their gametes at the apex of the climb, and rapidly swimming down again, an event taking no more than 2-3 sec. This event was preceded by at least 5 min. of courting during which the male made several "dummy ascents" by himself. This pair spawning and pelagic dispersal of eggs is presumably the normal mode of spawning in this species.

#### 4.3.4 *Pseudolabrus psittaculus*

4.3.4.1 *Sexual system*: The gonads of 51 individuals were histologically examined to determine the sexual system of this species. Of these, 23 were IP females, 27 were TP males, and one was transitional, with TP coloration. All males were secondary, with a residual ovarian lumen in the testes (Fig. 4.17c). Initial phase males are probably rare or absent in this species as none were detected from the sample of 51 individuals examined, and likewise, IP secondary males are probably absent or rare as well, as none were detected in the 23 IP fish examined. The sexual system in this species therefore appears to be monandric protogynous hermaphroditism, with no IP males.

This species is sexually dichromatic, with the males base coloration of pinkish-red being less intense than the females coloration. Males also possess approximately five longitudinal yellow lines which are absent in the females, while females and juveniles have a conspicuous black saddle at the posterior base of the dorsal fin, which is absent in males. This sexual dichromatism is diagnostic for primary sexual condition (Figs 4.14 and 4.15) with the colour phase always correctly predicting sex. This relationship

enabled a comparison of the length at sex inversion between fish captured at the Arch Rock site (Fig. 4.16) and those collected at the East Coast sites (Fig. 4.15) based on external coloration, a comparison which indicated that sex inversion occurred within a similar size range at both areas (18.5-20.5 cm). This size range corresponded to ages 5+ to 7+ (in February) at the East Coast sites.

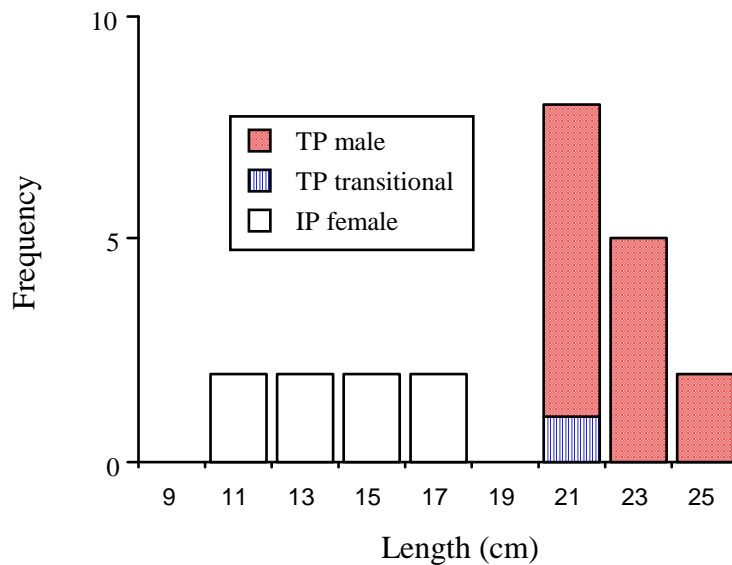


Figure 4.14 Frequency histogram of the *Pseudolabrus psittaculus* length/sex relationship of fish collected from the East Coast sites in February 1994, based on histological examination of fish.

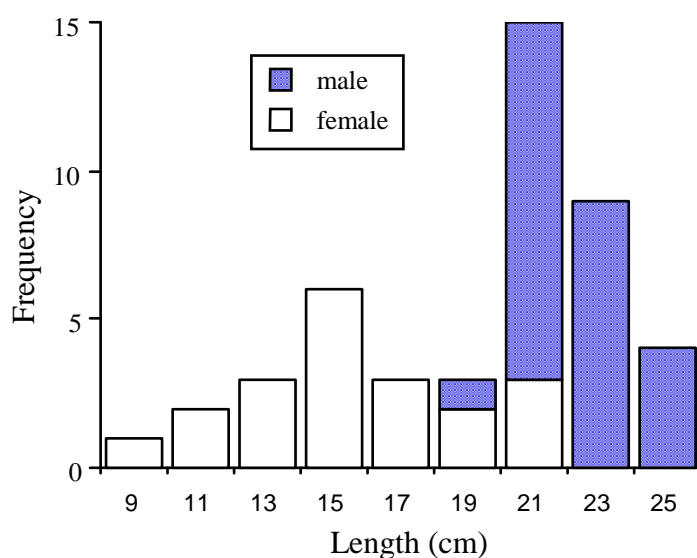


Figure 4.15 Frequency histogram of the *Pseudolabrus psittaculus* sex/length relationship based on external coloration of fish collected from the East Coast survey in February 1994.

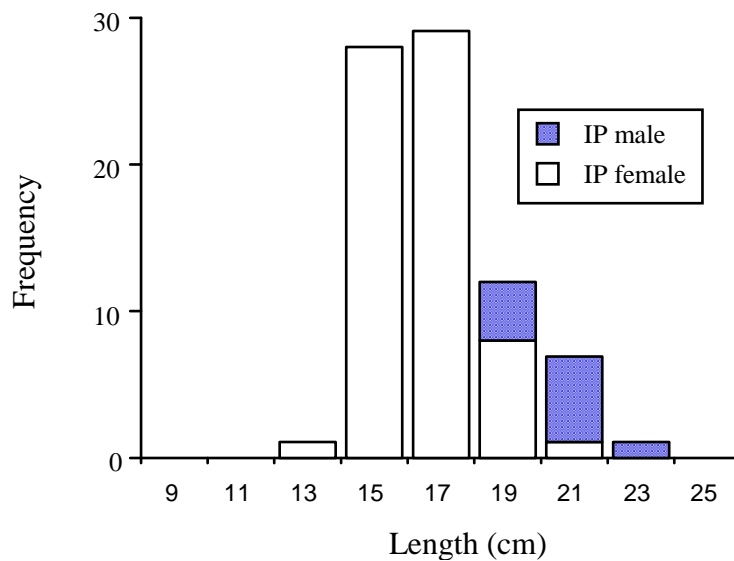


Figure 4.16 Frequency histogram of the *Pseudolabrus psittaculus* sex/length relationship, based on fish collected in fish traps at Arch Rock, Tasmania between September 1992 and January 1994.

4.3.4.2 *Histology*: In Fig. 4.17 the three main stages in the transition from ovary to testes are shown. Ovaries were found in all IP fish, and a post-spawning ovary collected in April, is shown in Fig. 4.17a. A transitional gonad was found in one TP fish (Fig. 4.17b), and had a typical transitional structure, with atretic oocytes and packets of spermatocytes and spermatids. Testes were found in all but one TP fish, and all testes had a large residual lumen, characteristic of secondary development (Fig 4.17c).

4.3.4.3 *Reproductive behaviour*: Males of this species are territorial, while females have small home ranges which overlap the ranges of a number of other females and 2 or 3 males (Chapter 2). At Arch Rock, males were observed actively courting females from mid-August to mid to late January, and presumably this corresponds to the duration of their spawning season, although spawning was never observed. Spawning is probably pelagic however, as no nest guarding or other behaviour associated with demersal spawning was ever observed.



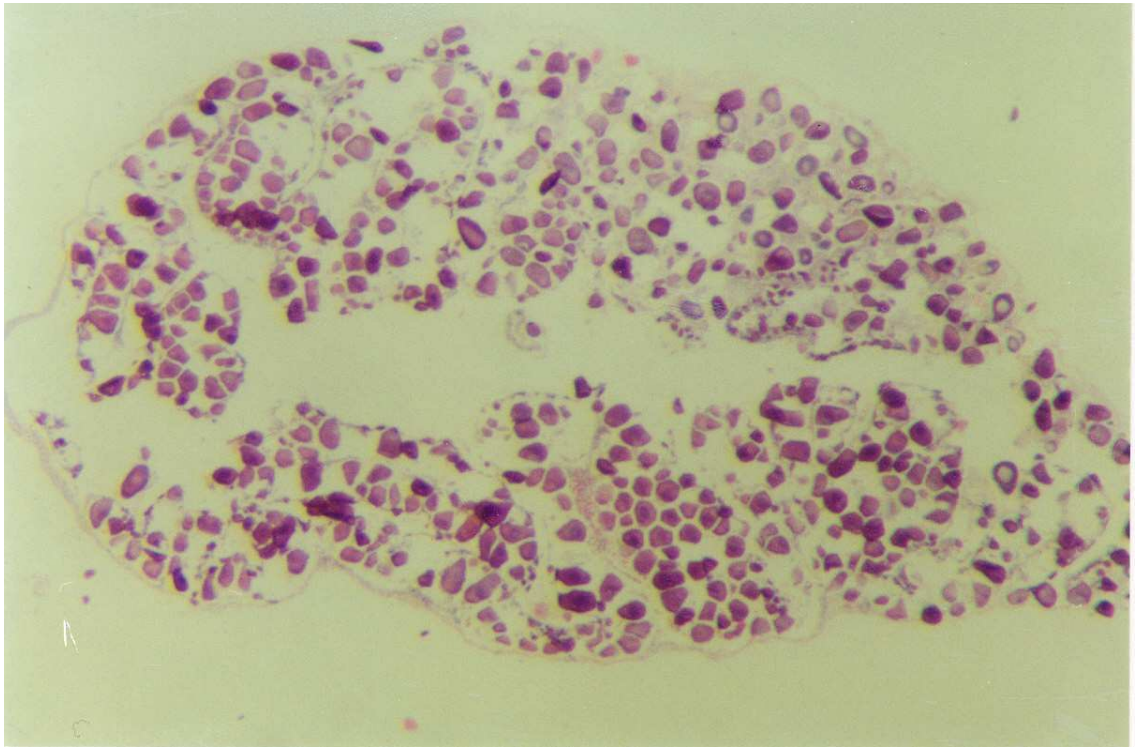


Figure 4.17a Low power TS of the ovary of a *Pseudolabrus psittacus* female, collected in April 1993, showing previtellogenic oocytes. Scale 1 cm = 330  $\mu$ m.

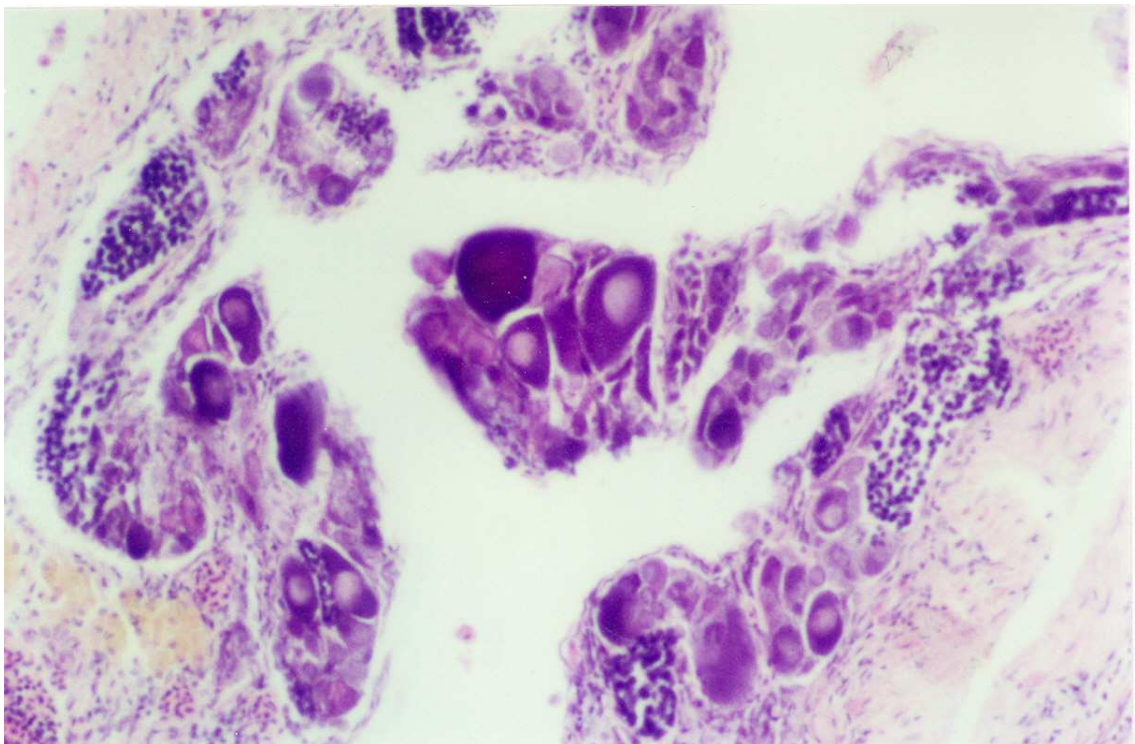


Figure 4.17b High power TS of the gonad of a transitional *Pseudolabrus psittacus* collected in February 1994. Note the clusters of spermatocytes and spermatogonia distributed amongst the residual oocytes. Scale 1 cm = 33  $\mu$ m.

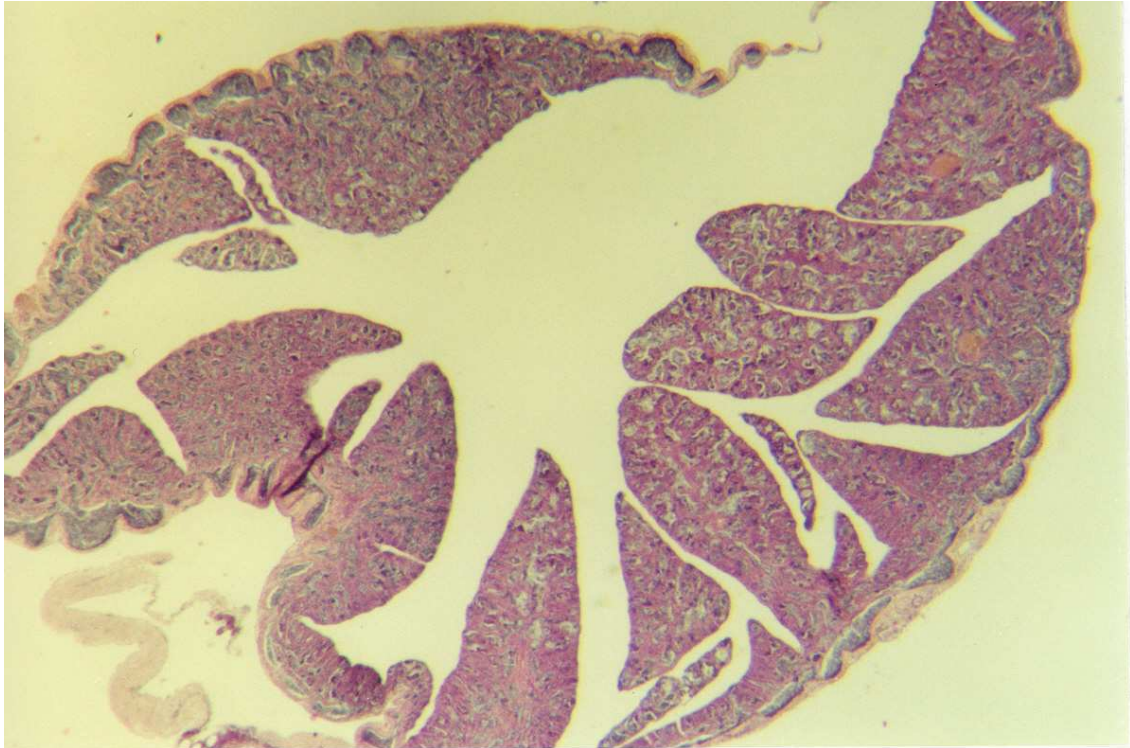


Figure 4.17c Low power TS of a testis of a *Pseudolabrus psittaculus* male, collected in February 1993. Note the residual lumen, a characteristic feature of protogynous sex inversion, as well as the peripheral secondary vas-deferens containing spermatozoa which have stained dark blue. Scale 1 cm = 330  $\mu$ m.

#### 4.3.5 *Penicipelta vittiger*

4.3.5.1 *Sexual system*: The sexes of individual fish were determined for 162 fish collected from the Huon region, Tinderbox and East Coast surveys, with histological sections being prepared for 13 males and 22 females. The typical male and female gonad structures are shown in Fig. 4.18. All males examined were found to be primary males, and all individuals examined during the breeding season with female coloration were females, indicating that this is a gonochoristic species. Further evidence for gonochorism was obtained from the East Coast survey, where all individuals collected were able to be sexed from fresh gonads. Of the 143 fish examined, 71 were female and 72 were male, indicating the sex ratio was not significantly different from unity ( $\chi^2 = 0.003$ ,  $p = 0.95$ ).



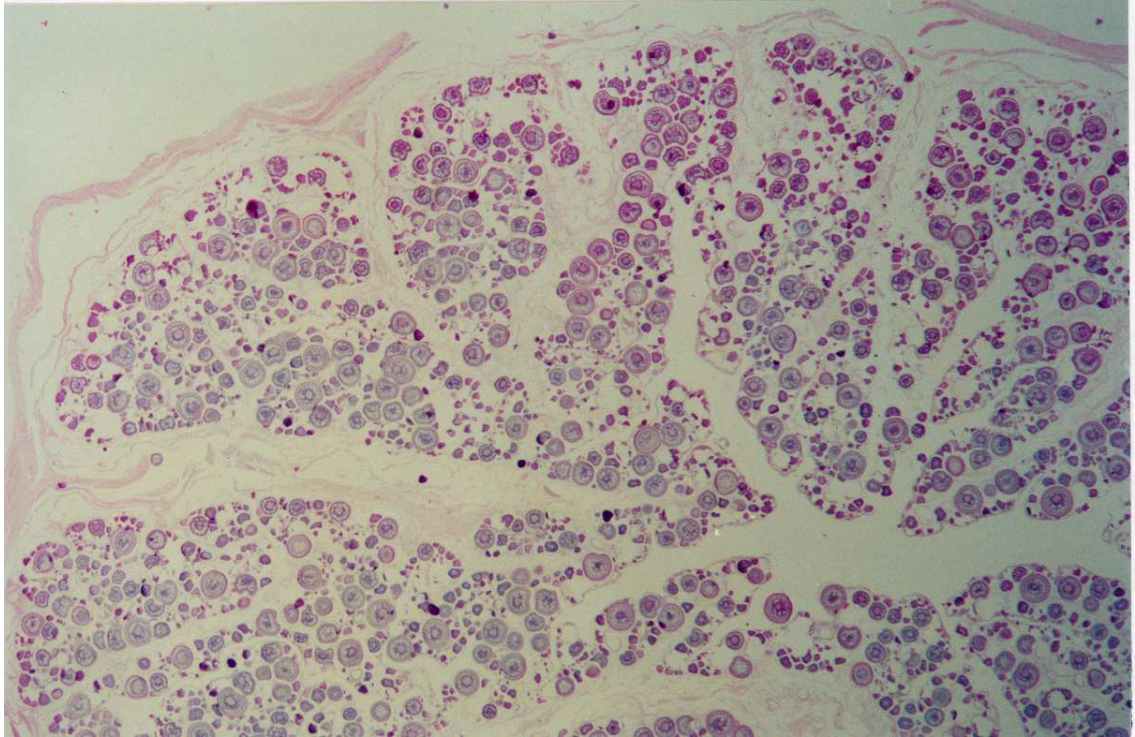


Figure 4.18a Low power TS of the ovary of a mature *Penicipelta vittiger* female collected in August 1993. Oocytes are in the early stages of vitellogenesis. The variety of oocyte diameters suggests that this is probably a sequentially spawning species. Scale 1 cm = 600  $\mu$ m.

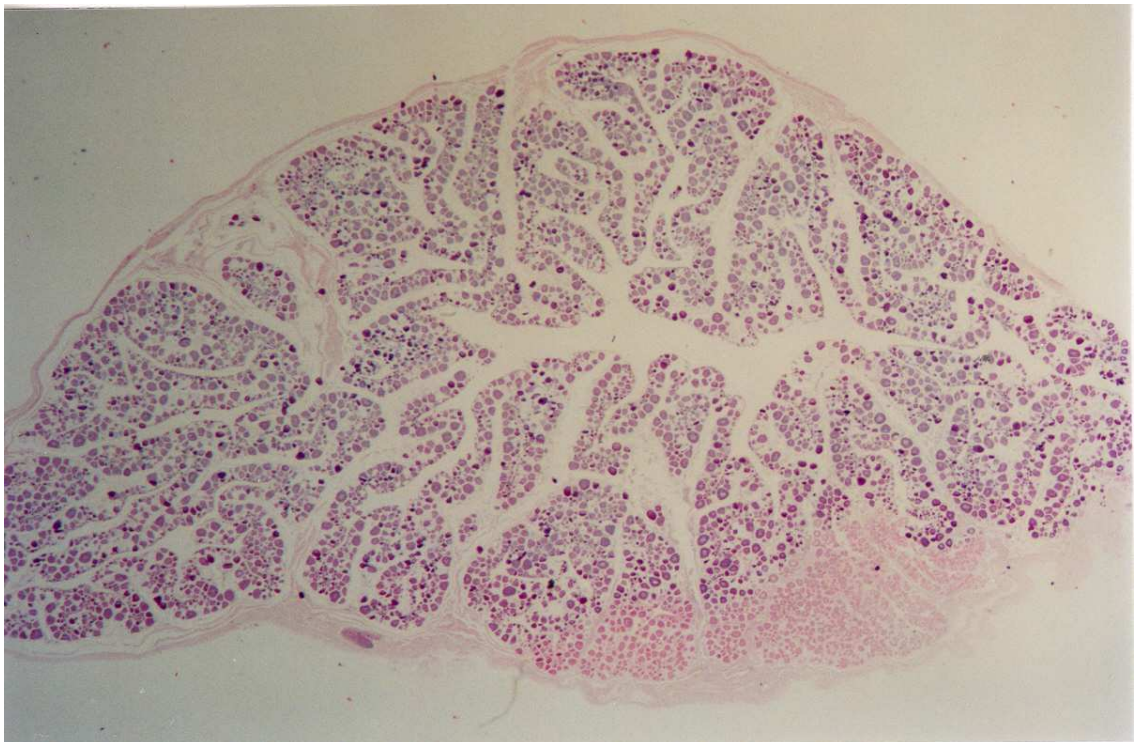


Figure 4.18b Low power TS of the ovary of an immature *Penicipelta vittiger* female, collected in August 1993. All oocytes are previtellogenic. Scale 1 cm = 600  $\mu$ m.

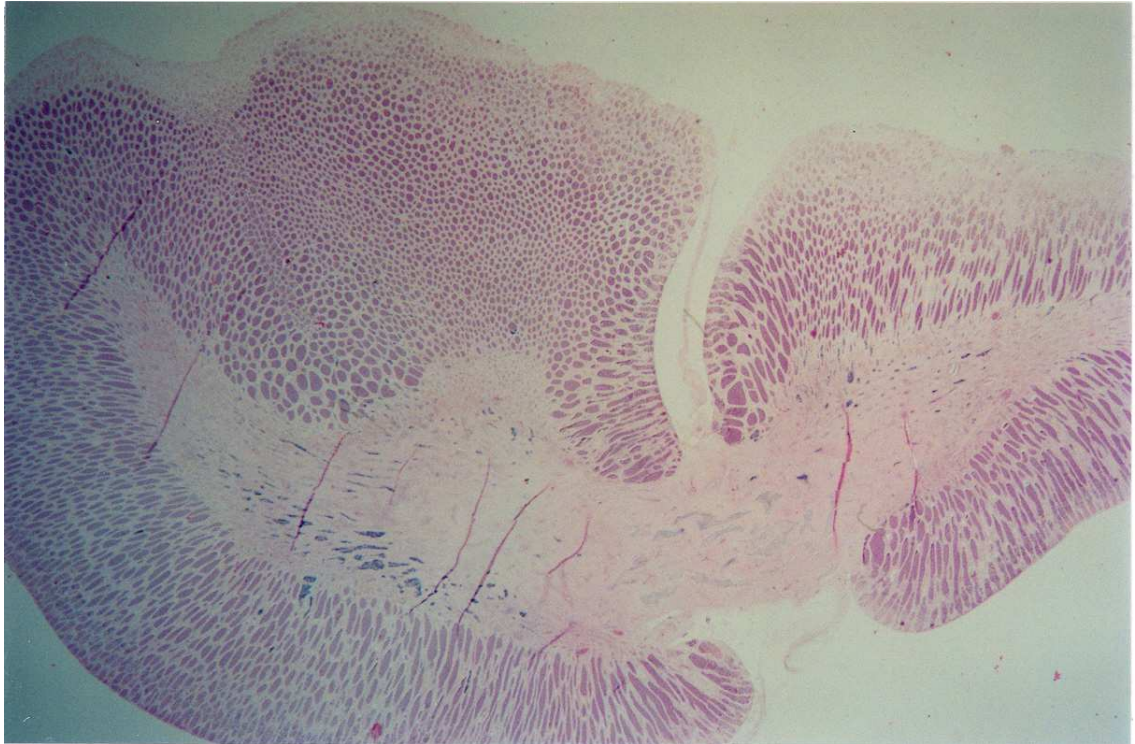


Figure 4.18c Low power TS of a testis of a mature *Penicipelta vittiger* male. Note the solid construction of the primary testis, with mature spermatozoa in the central vas-deferens. Spermatozoa are stained dark blue. Scale 1 cm = 600  $\mu$ m.

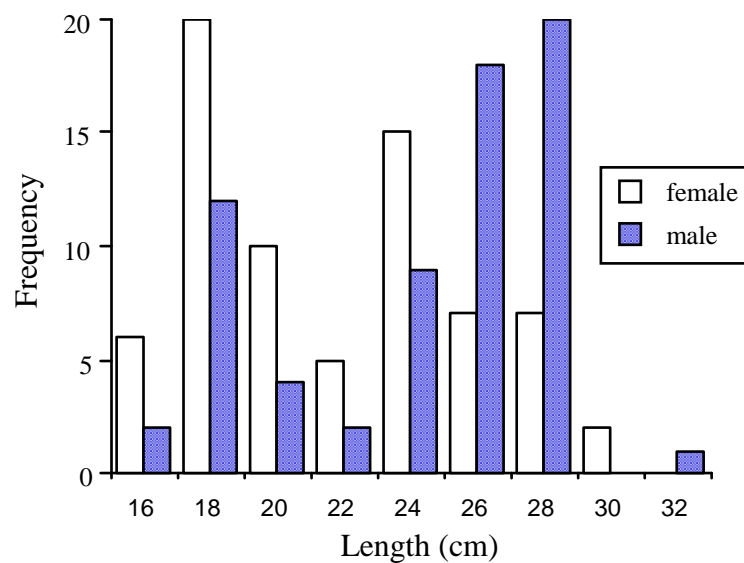


Figure 4.19 Frequency histogram showing the length frequency by sex distribution of *Penicipelta vittiger* individuals collected in the East Coast collection in February 1994.



Regardless of the equal sex ratio, there was an uneven distribution of sexes in the length frequency distribution of fish collected from the East Coast (Fig. 4.19), and this is probably at least partly related to differences in the growth rate of males and females. Whilst this difference was not evident in juveniles, it was highly significant in mature fish (see Chapter 3).

Examination of the raw GSI of fish sampled in the East Coast collection (Fig. 4.20) indicated that sexual maturity is not reached until attaining a length of approximately 22 cm and an age of 2+ years. This relationship could not be confirmed by histological analysis of East Coast ovaries as all had completed spawning. However, examination of ovaries collected at Tinderbox in August 1993 found oocytes in advanced stages of vitellogenesis in 2+ females ( $n = 2$ ), whereas no evidence of vitellogenesis as evident in 1+ females ( $n = 3$ ). Examples of mature and immature ovaries are shown in Fig. 4.18a and Fig. 4.18b, respectively.

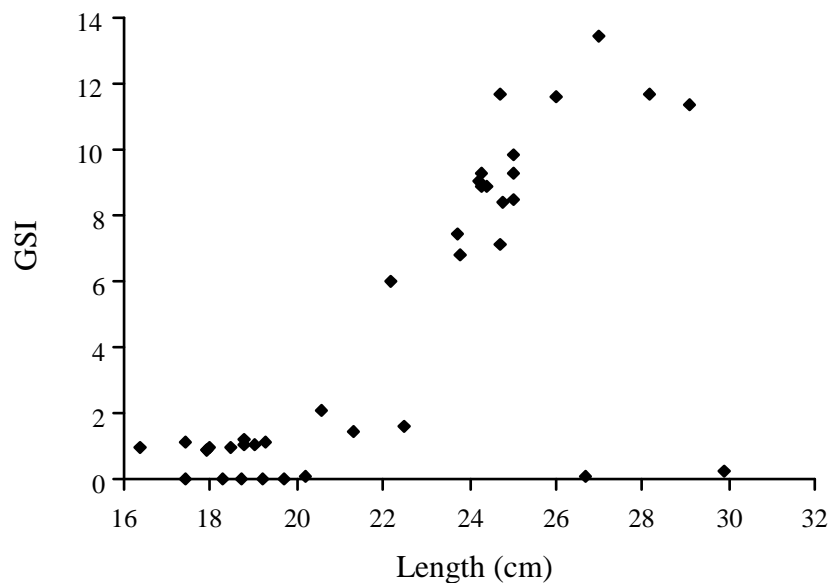


Figure 4.20 Relationship between length and raw GSI in *Penicipelta vittiger* females collected in February 1994 in the East Coast collection.

During the spawning season juvenile males were always differentiated from females by the presence of occasional iridescent blue spots on the head and belly. These distinguishing characteristics were still found in individuals collected from the East Coast in February, but were mainly absent from ones collected in the Huon region in April. Mature fish were strongly sexually dichromatic, and dimorphic, with females generally having a uniform coloration of white to yellow to orange, while males had a similar ground colour, but with much of the body extensively ornamented with iridescent blue lines and dots, the colour of which intensifies during the breeding season. Males also had a cluster of brush-like bristles just anterior of the caudal peduncle, although these bristles appear to degenerate after the breeding season.

4.3.5.2 *Reproductive behaviour*: *Penicipelta vittiger* is a home-ranging species. Males are not territorial, and their ranges overlap those of numerous other males and females (Chapter 2). Males were observed courting females from August to January, a behaviour which usually consisted of swimming alongside or behind the female, occasionally nudging or nipping at her belly and "fluttering". This fluttering involved contracting the body in vigorous spasms that lasted for approximately 5 sec. Females usually either ignored the males or actively tried to avoid them. While males were regularly involved in chases with other males the chases were never related to any form of territorial behaviour. Spawning was never observed, but presumably is pelagic as behaviour associated with nest guarding or demersal egg maintenance was never observed.

#### 4.3.6 *Meuschenia australis*.

4.3.6.1 *Sexual system*: A total of 103 *M. australis* were collected in the Huon region and East Coast surveys. All were sexed by inspection of fresh gonads, and of these, 12 female and eight male gonads were prepared for histological examination. All males were primary males and all individuals with female coloration were females. Therefore, it can be concluded that *M. australis* is a gonochoristic species.

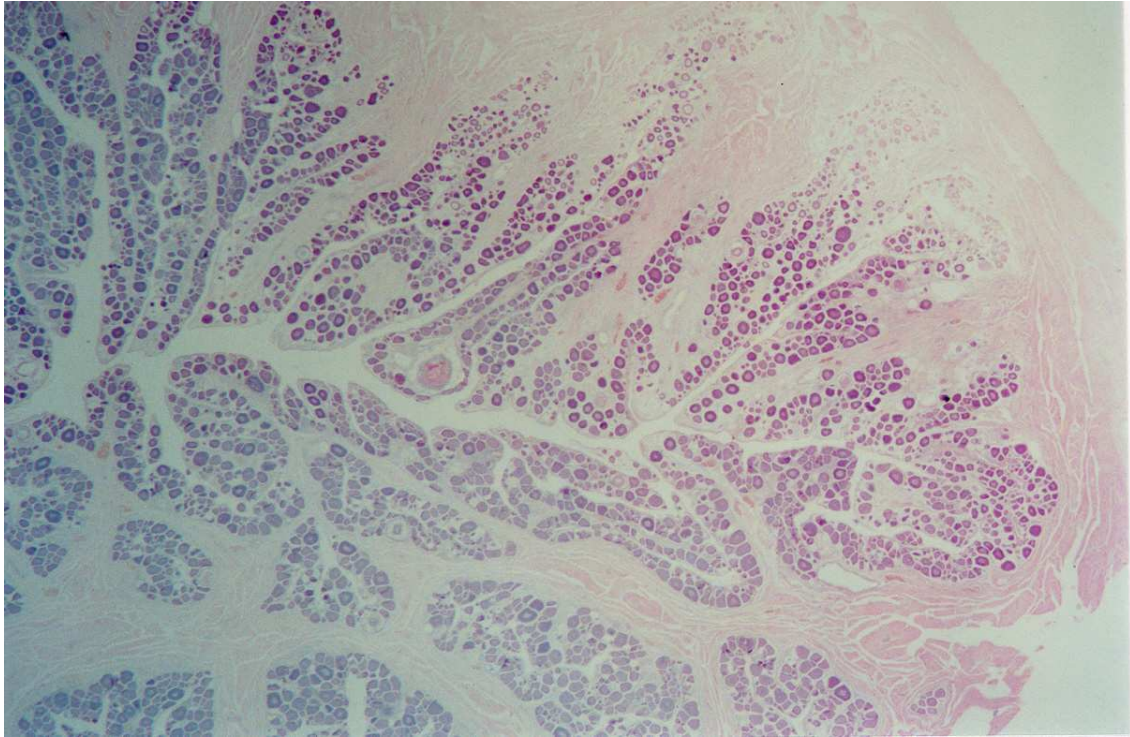


Figure 4.21a Low power TS of the ovary of a *Meuschenia australis* female, collected in April 1993. Scale 1 cm = 600  $\mu$ .

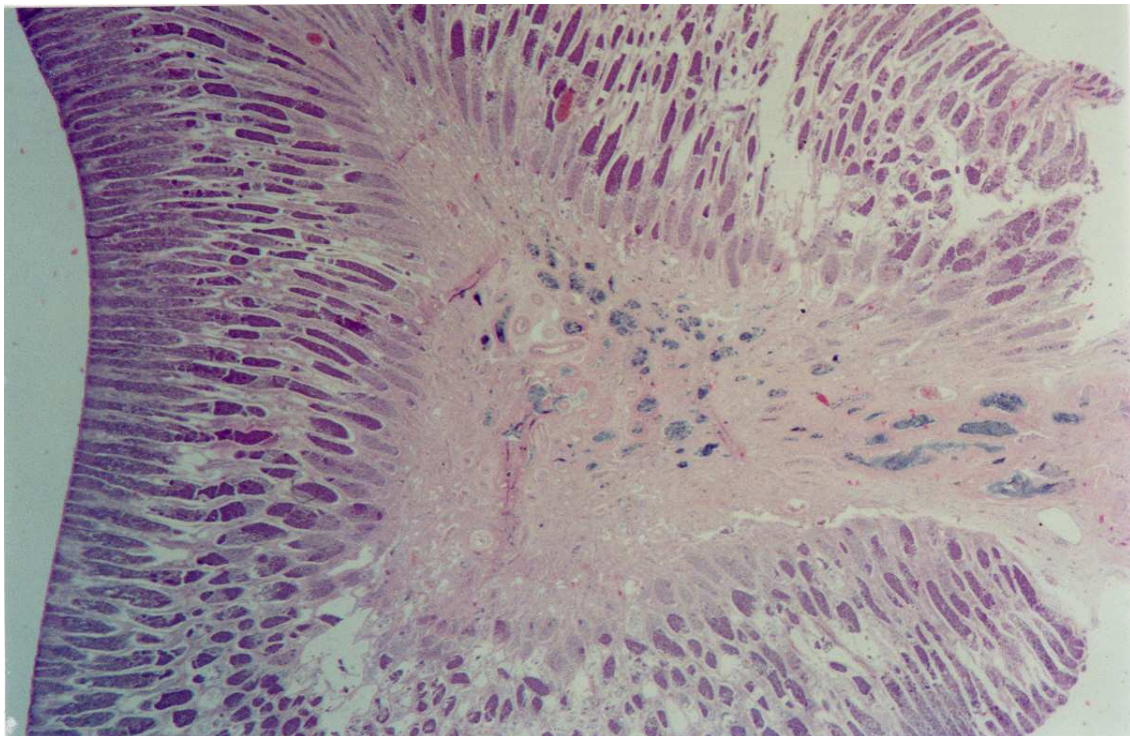


Figure 4.21b Low power TS of a testis of a *Meuschenia australis* male, collected in February 1994. Note the solid construction of the primary gonad, with spermatozoa (stained dark blue) in the centrally located vas-deferens. Scale 1 cm = 400  $\mu$ m.

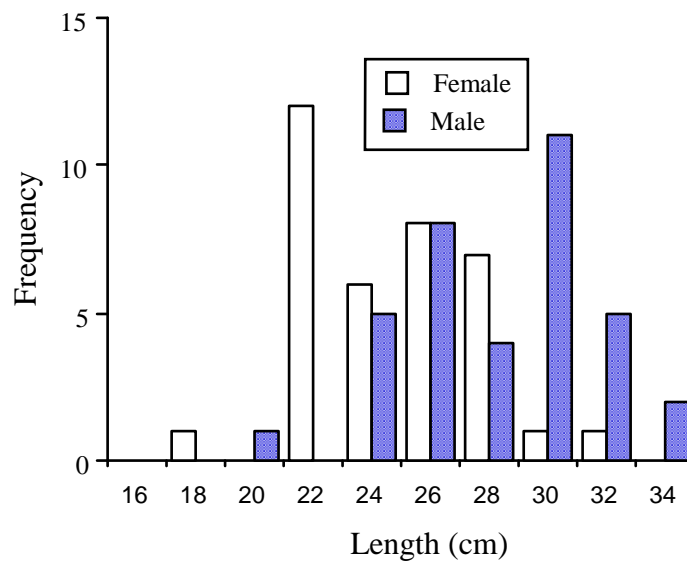


Figure 4.22 Frequency histogram showing the length frequency by sex distribution of *Meuschenia australis* individuals collected in the East Coast collection in February 1994.

The typical gonad structures are presented in Fig. 4.21, and Fig 4.21b shows the solid construction of the male testes, with central vas deferens, a construction which is characteristic of primary males.

Further evidence for gonochorism is given by the male to female sex ratio of 44 : 57 which is not significantly different from unity ( $\chi^2 = 0.61$ ,  $p = 0.43$ ). However, while the sex ratio may be even, there is a strong bias in the sex based length frequency distribution of fish collected in the East Coast survey (Fig. 4.22). This distribution is probably related to the faster growth of males of this species (Chapter 3) as well as the asymptotic growth pattern which was particularly evident in females. This species is sexually dichromatic, with the sexes of all individuals collected in this study being readily discernible from their colouration, even at the juvenile stage. Females always had numerous black spots on the head and belly which were always absent in the males.

4.3.6.2 *Reproductive behaviour*: While most individuals of this species are permanent residents of their home reef, they often range over large areas, potentially in excess of 1ha (Chapter 2). Each individual's range can overlap those of many others, regardless of sex, and there is no evidence of territorial behaviour (Chapter 2). Courting behaviour was infrequently observed due to this species low population density at Arch Rock, as well as its cryptic nature. At the adjacent Ninepin Point marine reserve where *M. australis* is more abundant, courting was observed from August to January, and this presumably corresponds to the duration of the spawning season. The reproductive behaviour usually consisted of the male either following or swimming alongside the female, and occasionally approaching her at right angles and nudging or nipping at her belly.

## 4.4 Discussion

### 4.4.1 *Spawning*:

In all of the six species examined in this study, reproductive behaviour was observed over at least a 5 month period from mid-August to mid-January. Although a more detailed histological study is needed, this period probably coincides with the duration of the spawning season. Such prolonged spawning periods appear to be common in temperate reef fish, including labrids, e.g. *Notolabrus celidotus* (Jones 1980), and *Centrolabrus exoletus*, *Crenilabrus melops*, *Ctenolabrus rupestris*, *Labrus berygylta*, and *Labrus mixtus* (Costello 1991), and monacanthids, e.g. *Monacanthus hispidus* (Hildebrand and Cable 1930), and have been reported for many New Zealand reef fishes by Doak (1972) and Thompson (1981), and some Tasmanian species by Gunn and Thresher (1991). The period during which spawning was observed in this study coincides with rising water temperatures and high levels of primary production, factors that could enhance the survival and growth of larval fishes. By spawning over such a long period these species can also ensure that at least at some time during the spring/summer period some of their offspring will be present in the water column during a peak in primary or secondary production. The advantages of such a spawning

strategy were highlighted in a study by Thresher *et al.* (1989) who found that transient pulses in primary production in Tasmanian waters usually preceded peaks in recruitment success of *Heteroclinus* sp. They suggested that such peaks in primary production, and associated peaks in secondary production, can have a profound affect on population ecology, especially recruitment success, as it may only be at such times that the availability of food in the water column rises above the threshold needed for maintenance and growth of newborn fish larvae. Species with a prolonged spawning period are much less likely to suffer the same extent of interannual variability in recruitment success as those that only spawn once and over a short period. Comparison of differences in the variability in recruitment success of synchronous and sequential spawning species with short and long spawning periods may prove to be a fruitful area for further research.

No evidence of demersal spawning was obtained for any of the species in this study, even though such behaviour is common in northern temperate labrids (Costello 1991) and is thought to be common amongst the monacanthids (Barlow 1987, Nakazono and Kawase 1993). The absence of demersal spawning in the labrids in this study, as well as those in New Zealand waters (Thompson 1981) suggests that the European benthic spawning species are unusual. There is no evidence of a general trend towards demersal spawning in temperate labrids from the pelagic spawning found in most tropical species. Furthermore, demersal spawning would not normally be predicted for such large fish under the size disadvantage hypothesis of Thresher (1984). This hypothesis suggests that while small fish may tend eggs in easily defended locations such as shells and small cracks in the reef, this becomes increasingly more difficult to do with increasing size due to decreasing agility and manoeuvrability. This hypothesis may also explain why the two large monacanthids in this study were not demersal spawners, although there are still too few studies of species in this family to ascertain whether pelagic spawning is, in fact, unusual.

### 3.4.2 *Labrid sexual systems*

Three of the four labrids examined in this study were identified as protogynous hermaphrodites, while *Notolabrus fucicola* is a secondary gonochorist. No primary or pre-maturational IP males were found in any of the hermaphrodite species, and where IP males were found, they were in the size range where sexual inversion would be expected, with the exception of three *N. tetricus* individuals collected at Ninepin Point in September 1990 (Fig. 3.2). It is likely that these particular IP males resulted from premature sex inversion, perhaps due to a temporary absence of larger males and females. At the time the collection was made, the site was being heavily netted by amateur fishermen prior to its declaration as a marine reserve, with the mesh sizes used selectively removing the larger fish.

Robertson and Choat (1974) proposed a model that predicted the presence of IP primary males in species with "loose" sexual systems which, when applied to labrids, would include species where harems are not maintained and males do not have the opportunity to become familiar with, and control, all the females in their territory. Under this model, all the hermaphrodite species in this study would be expected to have IP males, as all had a "loose" system, where the home ranges of females overlapped the territories of several males, thus limiting the control that males may exert. As no IP males were found, it appears that these three species, as well as *Labrus bergylta* (Dipper and Pullin 1979) are exceptions to the model. Another partial exception to this model is *Notolabrus celidotus* (Jones 1980) where primary males do not occur but a small proportion of IP pre-maturational males are present. Jones suggested that this may be a successful alternative strategy to primary males as it provides more phenotypic plasticity and a potentially greater response to the environmental conditions which may determine the fitness of a particular sex.

A similar phenotypic plasticity may explain the absence of primary males in *Pictilabrus laticlavius*, *Pseudolabrus psittaculus* and *Notolabrus tetricus*. If sex inversion in these species is determined primarily by social factors such as the density of males and an individual's position in a size structured hierarchy, then such a system may provide a more than sufficient response to changing environmental conditions, negating the need for IP males. This would be particularly the case if sex change can be rapid when necessary. Certainly this type of sexual transition process is common in the labrids, and was first documented by Robertson (1972) in *Labroides dimidiatus*, where transition of the most dominant female within a harem, from female to fully functional male, takes only 14 days from when the dominant male is removed.

In species with such a flexible system, living within an environment where males are able to maintain stable territories, initial phase males are unlikely to make a useful contribution to the reproductive success of a population, and would not be expected to form a significant proportion of the population. However, in species where sex change is determined by size or age, selection may favour the retention of some IP males as their fitness would increase dramatically during times of high mortality of older and larger fish. This may be particularly the case for species living in temperate environments which tend to be less stable than tropical ones and where occasional storms may have a great impact on population structure.

Further work is needed to determine the factors controlling sex inversion in both monandric and diandric species of labrids before more concrete models regarding the presence of IP males can be proposed. This work should particularly focus on monandric temperate species such as *Labrus bergylta*, *Pictilabrus psittaculus*, *Pseudolabrus psittaculus* and *Notolabrus tetricus*, and diandric temperate species with IP primary males such as *Labrus mixtus* and IP secondary males such as *Notolabrus celidotus*, so that any new model predicting the abundance of IP males can incorporate



the effects of social system "looseness" as well as latitude, and the degree of social control of sex inversion.

*Notolabrus fucicola* was unusual in that it is a secondary gonochorist, having a sexual strategy presently described for only one other species of labrid, *Oxyjulis californica*, by Diener (1976). This sexual system is obviously derived from protogynous ancestors, and must be the result of strong selection against TP males in favour of IP males. Some clues as to how this may have evolved in *N. fucicola* may be given by its preferred habitat. This species inhabits shallow waters along high energy coastlines. Because of the unpredictable nature of such a habitat, the territorial behaviour typical of this genus, and labrids in general, would be difficult to maintain, particularly during storms when fish need to move to deeper water to avoid being killed. The lack of territorial behaviour in this species is documented in Chapter 2. Without the social control that territorial behaviour enables, the proportion of IP males would be expected to increase, as predicted by Robertson and Choat (1974), or the average size of TP males would decrease due to lack of inhibition of sex change by dominant males. The resulting reduction in both the abundance and size of females would be maladaptive, and it would be expected that selection would favour a convergence with a gonochoristic system, where sexes were genetically determined. Such a system appears to be an optimal strategy for non-territorial reef fishes, as it is the system used by the majority of them.

In a book on the coastal fish of north-eastern New Zealand, Thompson (1981) reported that in New Zealand a small proportion of mature *N. fucicola* females change sex. If the observations reported by Thompson (1981) are correct, the mode of reproduction in the New Zealand population differs from that observed in the Tasmanian population. Such a difference between populations could be explained by their physical isolation by distance (limiting gene flow), with the New Zealand population representing an earlier and intermediate stage in the evolution of this species from an hermaphroditic ancestor. It may also explain the confusion in the literature on the sexual system of this species.

#### 4.4.3 *Monacanthid sexual system:*

Both *Meuschenia australis* and *Penicipelta vittiger* are gonochoristic. This was not unexpected as hermaphroditism has not previously been reported in this family or the related balistids (Thresher 1984). The initial confusion as to whether or not these species were gonochoristic arose because of the highly variable coloration found in both species, and the fact that differences in secondary sexual characteristics such as coloration are not readily evident in *P. vittiger* until sexual maturity is approached. While the sexes of 1+ juveniles of this species could be recognised during the breeding season due to the intensification of slight differences in external coloration, this was not the case in March/April once these differences faded. Mature fish of both species however, were distinctly sexually dichromatic, and, in the case of *P. vittiger*, sexually dimorphic. A less distinct sexual dimorphism was also observed in mature *M. australis*, with females being deeper in the body with respect to length, although this remains to be described in a taxonomic study.

There is a significant difference between the sexes in the growth rates of both species (Chapter 3). Males have a greater length at age by 2+, and generally attaining greater maximum length overall, although in *P. vittiger* growth rate differences were not evident in 1+ juveniles in February, and probably develop as maturity is approached and females apportion a greater proportion of their resources to reproductive effort. These differences between the sexes appear to be a characteristic feature of the monacanthids (Thresher 1984, Nakazono and Kawasee 1993) although in some species these differences may only be subtle ( e.g. *Oxymonacanthus longirostris*, Barlow 1987).

## **Chapter 5   Interannual variation in growth**

### **5.1 Introduction**

Interannual variability in growth rates has now been described in numerous fish species, ranging from small reef dwelling damselfish (Thresher 1983, 1985; Pitcher 1992) to large, commercial trawl species such as hake (e.g. Smith *et al.* 1990; Welch and McFarlane 1990), although the literature is dominated by studies on the commercially exploited species. These species include snapper (Francis 1992, 1994), cod (Joergensen 1992), plaice (Bergman *et al.* 1988; Rijnsdorp *et al.* 1991), sole (Marchand 1991; Kreuz *et al.* 1982; Peterman and Bradford 1987), haddock (Ross and Nelson 1992), flounder (Francis 1988) and rockfish (Boehlert *et al.* 1989; Woodbury and Ralston 1991).

While the cause of the interannual variation in growth is not clearly identified in most studies, it is usually attributed to either differences in water temperature (e.g. Smith *et al.* 1990; Woodbury and Ralston 1991; Francis 1994; Marchand 1991) or variation in stock density (e.g. Boehlert *et al.* 1989; Ross and Nelson 1992), although good correlations often exist with other oceanographic features such as upwelling (e.g. Kreuz *et al.* 1982). Temperature variation may be expected to contribute to growth variation in most fish species because of the direct relationship between temperature and metabolic rate, as well as the many factors that covary with temperature, such as water column productivity, a factor that may be important where growth is at least partly limited by food availability. Stock density can contribute to variation in growth primarily because many fish populations are believed to be resource limited and, therefore, as population density increases, the relative resource availability decreases.

The contribution that factors such as temperature make to growth may vary significantly with age, with growth in larval and early juvenile fishes being particularly more sensitive than adults to variation in temperature (e.g. Woodbury and Ralston 1991; Francis 1994). This age-based relationship could also apply to population density. However, in larval fish this is difficult to document as the influence of stock density on growth can easily be confounded by that of temperature or other factors. For example, Houde (1987) demonstrated that the doubling of instantaneous larval growth could result in a 100x increase in the survivorship of larvae, a relationship that could be incorrectly interpreted as implying growth is faster at higher population densities.

The degree to which growth displays density dependence probably depends upon relative stock abundance. Ross and Nelson (1992) showed growth was more highly correlated with stock abundance during periods when abundance is high than when it is low. Therefore many highly exploited and depleted stocks would not necessarily be expected to show a significant relationship between growth and stock density.

A range of techniques have been used to examine interannual variation in growth. Historically, most studies have used cohort analysis, or ages estimated from hard-part analysis, to generate length/age relationships that are compared between years (e.g. Smith *et al.* 1990; Welch and McFarlane 1990). A few have used annual growth increments derived from recapture of tagged fish (Francis 1988, 1992). Tagging has the advantage that it is a more direct method, and as long as fish are recaptured close to one year after tagging to avoid errors caused by seasonal effects on growth, this method is less prone to errors caused by assigning individuals to the wrong age classes or cohorts. More recent developments have included: (1) the discovery and use of daily growth rings in otoliths, enabling better comparison of growth in the larval and early juvenile stages of life (e.g. Woodbury and Ralston 1991; Francis 1994), and (2) the back calculation of population growth from otolith annuli of older fish, using the relationship between annuli radius and fish length (e.g. Boehlert *et al.* 1989). The latter method

allows interannual variability in growth to be back calculated from a single sample of fish collected at one location in one year, at least for species that live for several years. Both this method and tagging have an advantage over other methods in that it is known that it is variation within the one population that is being measured rather than the possibility that exists in many studies that the results are being confounded by spatial variation in growth, particularly where samples are obtained from a fishery.

This study examines interannual variation in growth in natural populations of temperate reef fishes, and the magnitude of this variation. Interannual variation in growth rate in mature populations of up to 240% has been reported by Francis (1992), and variation of such magnitude would impact on the usefulness of tag-based growth estimates for validation of the use of otolith annuli for ageing. A further aim of this study was to test the hypothesis that as reef fishes live in a complex habitat with a wide array of potential food items available to them, they may be less susceptible to interannual growth variation than many of the commercial species studied so far, which are usually found in much simpler habitats, and rely on far fewer food species. In this study, interannual growth variability was examined over 4 years in the labrid *Notolabrus tetricus*, and over 3 years in the labrid *Notolabrus fucicola*.

## **5.2 Materials and Methods**

This study was conducted at Arch Rock, Tasmania (Fig. 2.1) in conjunction with the long and short-term movement study presented in Chapter 2, and the growth study presented in Chapter 3. The methods of tagging, and sizes of fish tagged, are described in these chapters. Six species were regularly tagged throughout the study period; however, four of these (*Pictilabrus laticlavius*, *Pseudolabrus psittaculus*, *Penicipelta vittiger*, and *Meuschenia australis*) were not recaptured in sufficient numbers to allow comparison of growth between years. In the case of *M. australis*, sufficient individuals would have been recaptured if it were not for the significant sex-related differences found in the growth rates, and the strongly asymptotic growth curves which complicated

analysis. Sufficient recaptures were made on *Notolabrus tetricus* to allow interannual growth variability to be assessed over a 4 year period between December 1990 and December 1994, and on *N. fucicola* for a 3 year period between December 1990 and December 1994. The period during which growth was measured each year was from 1 December to 30 November. In a similar manner to the methods used in Chapter 3, only length increments from fish at large for a period of 10 to 14 months were used for analysis. These measured increments were then adjusted pro-rata to estimates of 12 month growth. Length increments from fish captured during longer and shorter periods were not used due to the increased contribution of measurement errors in short-term recapture based estimates, the likely effect of seasonal variation in growth on pro-rata estimates of annual length, and also the loss of resolution of interannual differences which would occur if growth periods were allowed to overlap substantially. These limitations restricted the number of recaptured fish available for analysis, particularly during the years 1992-93 and 1993-94 where less time was available for fieldwork. The interannual variability in the relationship between Length (year 1) and Length (year 2) was examined by ANCOVA, using the MGLH/ General Linear Model function of the computer statistical package SYSTAT (version 5.2 for Macintosh). Where the slope term (year\*x interaction) was not significant, and  $P > 0.25$ , the ANCOVA was repeated after deleting the interaction term from the model to increase the power of detecting differences in elevation. In the case of *N. tetricus*, where some interannual variability was detected, the difference between years in the means of the annual length increment of fish ranging from 18-32 cm in length, were examined by ANOVA using the MGLH/ Fully Factorial (M) ANOVA function of SYSTAT. For this analysis for both species, only fish with initial lengths between 18 and 32 cm were used in each recapture period to minimise the influence of length related differences in growth rates on the results.

### **5.3 Results**

#### **5.3.1 *Notolabrus fucicola***

After an examination of the residuals indicated that analysis of the growth results using untransformed data was appropriate (Figure 5.1), the interannual growth rate data was analysed by ANCOVA (Table 5.1a). This indicated that there were no significant differences in growth between years, even after the analysis was repeated following removal of the non-significant "year\*x" term (Table 5.1b). This lack of significant interannual growth variation was expected, as a plot of the regressions of length in year 1 against length in year 2 for the three year's growth showed that there was little difference in either elevation or slope between years (Fig. 5.2), and the mean annual growth increment of fish with initial total length of 18-32 cm was also remarkably similar between years (Table 5.2).

Table 5.1 One factor ANCOVA of interannual variation in growth of tagged *Notolabrus fucicola* at Arch Rock, where x = length in year x, and y = length in year x+1. (n = 82,  $r^2 = 0.98$ )

(a) Slope term included (year\*x)

Source	SS	DF	MS	F	p
year	0.4	2	0.2	0.64	0.53
x	729	1	729	2341	<0.01
year*x	0.5	2	0.2	0.81	0.45
error	23.7	76	0.3		

(b) Slope term excluded. Test of elevation only.

Source	SS	DF	MS	F	p
Year	0.4	2	0.2	0.61	0.55
x	1816	1	1816	5858	<0.01
error	24.2	78	0.3		

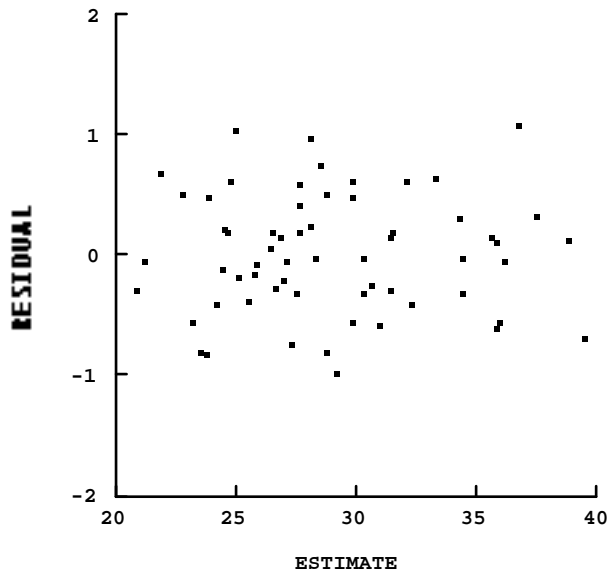


Figure 5.1 Residuals plot from the one factor ANCOVA of interannual variation in growth of *Notolabrus fucicola* shown in Table 4.1(a) and using untransformed data.

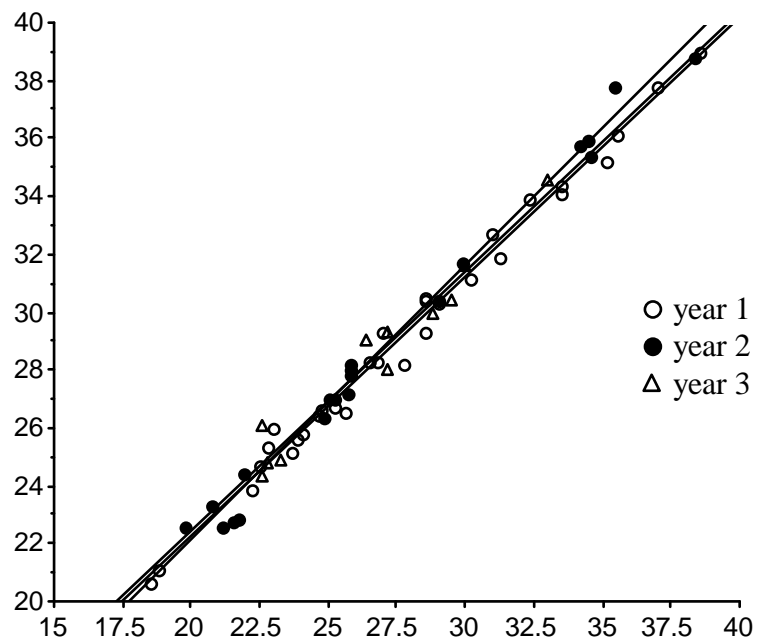


Figure 5.2 Linear regressions of yearly growth of tagged *Notolabrus fucicola* at Arch Rock showing the degree of interannual variation in growth rate, and plotted as length in year  $x$  against length in year  $x+1$ , for the three years Dec. 1990-91, Dec. 1991-92, Dec. 1992-93.



Table 5.2 Yearly mean growth increment ( $\pm$  s.e.), and mean length ( $\pm$  s.e.) of tagged *Notolabrus fucicola* individuals with initial total fish lengths of between 18 and 32 cm, at Arch Rock, Tasmania.

Year	1990-91	1991-92	1992-93
Mean increment (mm)	17.7 (0.09)	19.0 (0.13)	18.0 (0.26)
Mean length (cm)	25.87 (0.72)	24.25 (0.78)	26.67 (1.06)
N	39	15	10

### 5.3.2 *Notolabrus tetricus*

An initial examination of the untransformed data by ANCOVA revealed no evidence of slope differences between years (Table 5.3a,  $p = 0.35$ ). While there was some slight shape to the residuals plot (Fig. 5.3), with variance decreasing with increasing total length, this was not able to be further improved by any appropriate data transformation. When the data were re-analysed after removing the non-significant interaction term "year\*x" from the model, the term "years" was significant (Table 5.3b,  $p = 0.014$ ), suggesting that there was some interannual variation in growth, and that this difference was fairly constant over the size range examined.

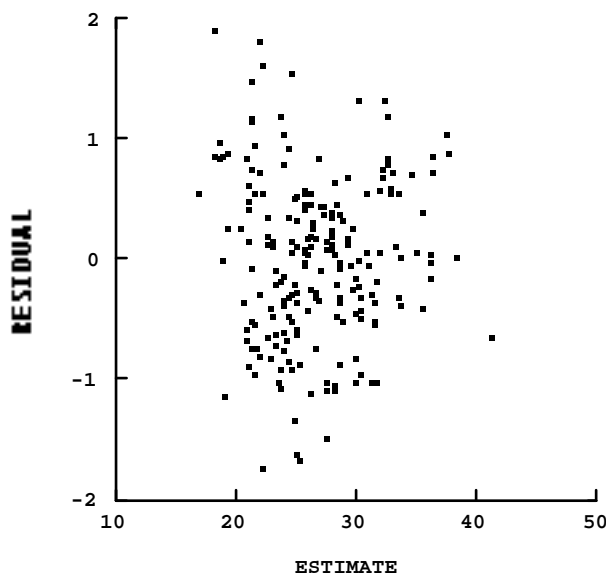


Figure 5.3 Residuals plot from the one factor ANCOVA of interannual variation in growth of *Notolabrus tetricus* shown in Table 5.3(a) and using untransformed data.

Table 5.3 One factor ANCOVA of interannual variation in growth of *Notolabrus tetricus*, where  $x$  = length in year  $x$ , and  $y$  = length in year  $x+1$ . ( $n = 207$ ,  $r^2 = 0.98$ )

(a) Slope term included (year\* $x$ )

Source	SS	DF	MS	F	p
year	1.1	3	0.3	0.7	0.54
$x$	1770	1	1770	3639	<0.01
year* $x$	1.6	3	0.5	1.1	0.35
error	96.8	199	0.5		

(b) Slope term excluded. Test of elevation only.

Source	SS	DF	MS	F	p
year	5.2	3	1.8	3.6	0.014
$x$	4272	1	4272	8768	<0.01
error	98.4	202	0.5		

A comparison of the regressions of length in year 1 against length in year 2 for the four different years reveals this difference (Fig. 5.4), although it appears from this figure that the slope effects did make some contribution to the difference between years. Because there was some possibility that outliers at either end of the length range examined had unduly influenced the ANCOVA results, the results were further examined by ANOVA, comparing the means of the annual length increment of 18-32 cm length individuals between years. The yearly means are shown in Table 5.4, and the results of the ANOVA in Table 5.5. The ANOVA revealed a significant difference between years ( $p = 0.05$ ). The source of this difference was then examined by a Tukey test of the pairwise differences between the yearly means, which found that the only significant difference between years was between years 1990-91 and 1992-93 ( $p = 0.031$ ). If the mean estimates of yearly growth rate in each year shown in Table 5.4 are correct, this difference would be in the order of 23% between the two years. This difference does not appear to be related to the mean size of fish tagged during each period, as this size remained between 24.1 and 25.1 cm throughout the study (Table 5.4).

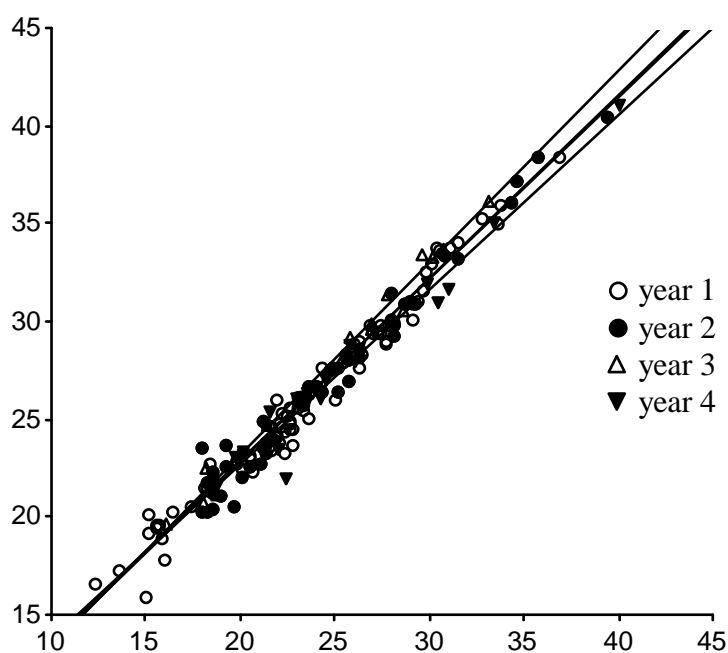


Figure 5.4 Linear regressions of yearly growth of tagged *Notolabrus tetricus* at Arch Rock, showing the degree of interannual variation in growth rate, and plotted as length in year x against length in year x+1, for the four years Dec. 1990-91, Dec. 1991-92, Dec. 1992-93, Dec. 1993-94.

Table 5.4 Yearly mean growth increment ( $\pm$  s.e.), and mean length ( $\pm$  s.e.) of tagged *Notolabrus tetricus* individuals with initial total fish lengths of between 18 and 32 cm, at Arch Rock, Tasmania.

Year	1990-91	1991-92	1992-93	1993-94
Mean increment (mm)	25.1 (0.7)	25.1 (0.12)	30.8 (1.7)	26.3 (1.6)
Mean length (cm)	24.29 (0.37)	25.19 (1.29)	25.12 (1.29)	24.11 (0.87)
N	113	40	13	16

Table 5.5 One way ANOVA of interannual variability in the annual length increment of tagged *Notolabrus tetricus* individuals with initial total fish lengths of between 18 and 32 cm, at Arch Rock, Tasmania.

Source	SS	DF	MS	F	p
years	3.99	3	1.33	2.63	0.05
error	89.00	178	0.51		

Estimates of the abundance of *N. tetricus* at Arch Rock between December 1990 and December 1994 were derived from the results of capture mark and recapture experiments each year, using simple Petersen estimates and are shown in Table 5.6. Abundance remained relatively constant at this site between December 1990 and December 1993, and then dropped by approximately 50% between December 1993 and December 1994. Changes in annual growth rate showed no correlation with abundance of this species, even in 1994 when stock density was reduced significantly.

Table 5.6 Annual estimates of the abundance of *Notolabtus tetricus* greater than 15 cm TL at Arch Rock, calculated by Petersen method using the results of intensive capture/mark/recapture exercises conducted in December and January of each year.

Year	1990-91	1991-92	1992-93	1993-94	1994-95
Number	320	290	321	346	138

Table 5.7 shows the mean annual water temperature corresponding to each of the recapture periods, and is based on the average of daily temperatures collected at 0 m and 5 m depth at a marine farm at Hideaway Bay, 12 km to the northwest of Arch Rock, a site and depth range considered to be representative of the conditions found at Arch Rock. When the relationship between mean annual growth increments and mean annual water temperature was examined (Fig. 5.5), a strong positive correlation was found ( $r^2 = 0.96$ ).

Table 5.7 Mean annual water temperature (in degrees Celcius) at Hideaway Bay, a site 12 km to the northwest of Arch Rock. Each annual period is taken from 1 December to 30 November. The temperature is calculated from the average of daily readings taken at the surface and 5 m depth by Huon Atlantic Salmon Pty Ltd.

Annual Period	12/1988- 11/1989	12/1989- 11/1990	12/1990 - 11/1991	12/1991- 11/1992	12/1992 - 11/1993	12/1993 - 11/1994
Mean temperature (C)	14.51	14.21	13.21	13.03	14.01	13.21

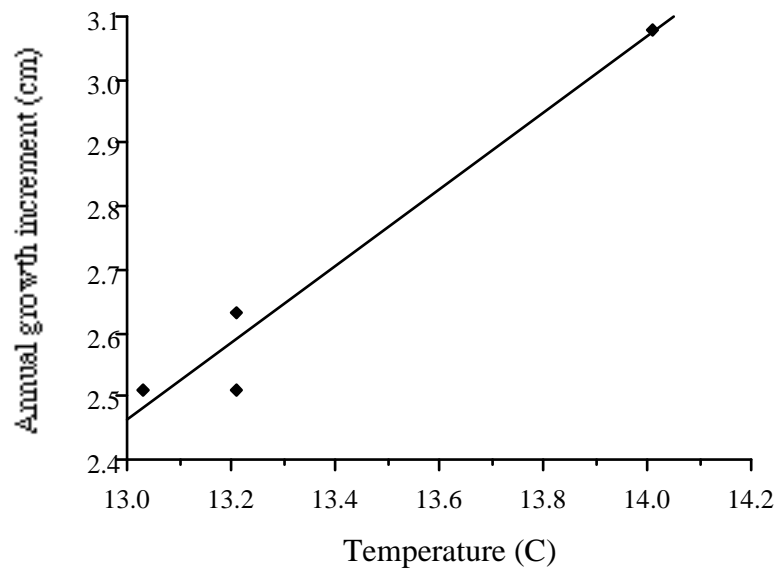


Figure 5.5 Relationship between annual growth increment and mean annual temperature for tagged *Notolabrus tetricus* at Arch Rock, Tasmania, in four consecutive 12 month periods beginning on 1 December 1990.

#### 5.4 Discussion

The extent of interannual variability in growth appeared to be minimal in this study. No difference between years was found in *N. fucicola* and only a slight difference between years was found in *N. tetricus*, where growth in the year 1992-93 was an average of 23% greater than in the year 1990-91. This difference was strongly correlated with temperature, a factor which has been shown to explain growth variability in a number of other species, including rockfishes (*Sebastes* spp.) (Woodbury and Ralston 1991), and snapper (*Pagrus auratus*) (Francis 1994). While an increase in temperature could have increased growth either directly by increasing metabolic rate, or indirectly through processes such as increasing the productivity of the reef, no data was collected to allow an examination of these possibilities.

Although the interannual growth variability in *N. tetricus* was correlated with temperature, the correlation was based on only 4 years of data, and several more years of data are needed before the significance of this relationship can be properly assessed.

It is possible that the observed growth variability could have also been related to a number of other unknown factors, as unexplained growth variability, unrelated to temperature or abundance, has been described in a number of other studies, even where annual growth rates have varied by up to 240% between years (e.g. Francis 1992). One possible explanation for such variation is strong interannual variation in recruitment and growth of prey species. This may be particularly the case for species which rely on only a limited number of prey species. An example may be the Arctic cod (*Gadus morhua*) where Joergensen (1992) detected a strong correlation between interannual growth rates and the cod to capelin ratio, where capelin are the principle dietary items of the cod. In reef species such as *N. fucicola* and *N. tetricus*, which are generalist feeders eating a wide range of items including molluscs, crustaceans and echinoderms, the impact of interannual variability in recruitment success and growth of dietary species is likely to be far less significant, because it would be unlikely that the recruitment success and growth of all prey species would be positively correlated. In such species, a more constant resource supply is likely to be maintained by living in a species rich habitat, and by having a generalist diet.

One other possible explanation for interannual growth variation is that interspecific competition for available resources may often be more important than intraspecific competition, and that growth is actually density dependant, where this density dependence is related to resource competition as a whole, rather than just within conspecifics. This is a possibility overlooked in the vast majority of studies, although Thresher (1983, 1985) explored this possibility in the planktivorous coral reef fish *Acanthochromis polyacanthus*, and found that interannual variability in growth of juveniles and adults was related to the abundance of resource competitors, specifically heterospecific planktivores. While a similar situation could have occurred with *N. tetricus*, it was not obviously related to the abundance of fish competitors, as *N. fucicola* and *M. australis* were the only species whose diets broadly overlapped that of *N. tetricus* at Arch Rock, and the abundance of these species remained relatively

constant over this period, and at low levels, with the average abundance of *N. fucicola* being approximately 80, and that of *M. australis* being approximately 50. There was also no obvious change in the abundance of invertebrates that may compete either directly or indirectly with *N. tetricus* for resources, although no attempt was made to quantify invertebrate abundances to detect such changes.

Regardless of the evidence of interannual variation in growth in *N. tetricus*, this growth variation was small, and was remarkably stable over the 4 years of this study, as was the growth of *N. fucicola*, with the results for both possibly indicating a trend for long-term stability of growth in many temperate reef fishes, at least for those with generalist diets, inhabiting reefs not subject to large interannual variations in mean temperature. Such a trend would not be completely unexpected, as many species, including *N. tetricus* and *N. fucicola* appear to spend the majority of their time either resting or being involved in various behavioural interactions with other fishes. A small change in their time budget would possibly be all that was necessary to counter the effects of most interannual variation in food resource availability. In times of super-abundance of food, or during food supplementation experiments, growth would be expected to increase because of opportunism. However, such events are probably rare in nature, and also short-lived as numerous other species are also likely to exploit such a resource. Far more work needs to be done to properly quantify the relationship between, and relative importance of, inter and intra-specific competition and growth in natural populations of reef fishes before the stability of growth in reef fishes can be properly assessed. Such work needs to especially concentrate on how the level of growth variability is related to differing levels of dietary specialisation, habitat complexity and time budgets.

The low levels of interannual growth variation detected in this study indicate that the use of tag-recapture data to validate the age/length relationship determined from hard-part analysis may be appropriate, and not unduly biased by growth differences between years. It also indicates that the estimates of growth by either method may be considered

as reasonably reliable estimates of average growth at this site for most years, rather than just a "snapshot" of growth over a particular time period. Unfortunately this only applies to *N. fucicola* and *N. tetricus* growth validation, as insufficient results were available to examine the magnitude of interannual variation in the remaining species. Obviously interannual variations in mean water temperature can at times have a significant impact on the growth rates of temperate reef fishes, and where tagging studies are used to estimate growth and age relationships this possibility should be considered in the experimental design. Further studies are needed to determine the extent to which growth rates can vary between years, particularly in locations subject to substantial variations in mean annual water temperature.



## Chapter 6 Spatial Patterns of Growth

### 6.1 Introduction

Long-term studies on assemblages of fishes on both temperate and coral reefs have demonstrated that the quantitative and qualitative composition of their constituent species varies significantly, both spatially and temporally, (e.g. Stephens and Zerba 1981; Choat *et al.* 1988; Carr 1989; Sale *et al.* 1994; Holbrook *et al.* 1995). There is, however, usually considerably more variation between habitats and locations than between years. Much of the spatial variation appears to be due to preferential settlement in favoured habitats and, perhaps, increased survival of new recruits in optimal habitats. This has been indicated in a number of studies, where the relative order of sites preferred by new recruits was shown to remain reasonably constant regardless of the magnitude or direction of changes in recruitment between years (e.g. Jones 1984a; Choat *et al.* 1988; Planes *et al.* 1993). In temperate regions, much of this spatial variation in recruitment has been related, either positively or negatively, to the occurrence and relative abundance of the kelp canopy (Jones 1984a; Carr 1989, 1994; DeMartini and Roberts 1990).

While there is now some agreement as to the main factors structuring spatial variation in recruitment, there is still considerable debate as to the causes of temporal variation. At present, there are at least six main models that have been proposed to explain community regulation of fishes on reefs. While most of these models have been developed and tested on coral reefs, they are equally likely to be important in explaining the processes occurring on temperate reefs as well. These models include

- (1) the niche diversification hypothesis, that proposes past or present interspecific competition for limiting resources structures the assemblage (e.g. Connell 1980)
- (2) the competitive lottery hypothesis of Sale (1974),
- (3) compensatory mortality and predation on common species (Connell 1978)
- (4) intermediate disturbance (Connell 1978)

(5) sources and sinks (Dale 1978) and

(6) recruitment limitation (e.g. Williams 1980; Doherty and Williams 1988a,b).

Evidence for and against each of these models has been extensively reviewed recently by a number of authors including Ebeling and Hixon (1991), and Jones (1991).

The models fall into two natural categories; these are (1) equilibrium models, where competition for resources structures the community either at, or after recruitment, and (2) non-equilibrium models, where recruitment limitation or predation (*sensu* Hixon 1991) limit the population to levels where competition is not an important structuring process.

While it is likely that no one model will be correct on all occasions, non-equilibrium models have received the most attention by researchers in recent years, in particular the recruitment limitation model. Under this model, reef fish populations are considered to be limited by the supply of post-larval recruits, such that in most circumstances the availability of new recruits is sufficiently low to maintain resident populations below the carrying capacity of their environment. The resulting surplus of resources would therefore ensure that competition for resources is not an important process in structuring populations and assemblages. The supply of new recruits is expected to be variable and unpredictable, at least in species with a dispersive larval stage, where mortality is reported to approach 100% in most species (Leis 1991). It is this variability that primarily structures the population.

In both temperate and tropical regions, the settlement of post-larval fishes has been reported to fluctuate significantly between years (e.g. Cushing 1977; Sale *et al.* 1984; Shulman 1985; Doherty and Williams 1988a) and could certainly provide a strong mechanism for structuring an assemblage. While the causes of these fluctuations remain relatively unknown, there is some speculation that, at least in temperate regions, the patchiness of larval food may be an important factor in determining larval survival,

particularly when yolk-sac reserves are exhausted. These ideas are incorporated into the match/mismatch hypothesis of Cushing (1975). Recent evidence suggests that at least in one small temperate reef species (*Heteroclinus* sp.) the coincidence of newborn larvae and episodic phytoplankton production pulses is an important factor in explaining recruitment levels (Thresher *et al.* 1989).

While there is a growing body of evidence supporting the recruitment limitation hypothesis (e.g. Doherty 1983, 1994; Victor 1983, 1986; Cowen 1985; Doherty and Fowler 1994), and the importance of recruitment in general in structuring assemblages (Sale *et al.* 1984), a number of other studies of both temperate and tropical fishes have found evidence that at least sometimes post-recruitment processes are also important. For example, in the temperate labrid *Pseudolabrus celidotus*, Jones (1984b) observed that adult numbers increased with increasing recruitment only up to a certain level, beyond which density dependant mortality and growth of juveniles became important factors limiting adult densities, primarily through competition between juveniles for food. Jones (1990) revealed a similar relationship through both manipulative and natural experiments on the tropical pomacentrid *Pomacentrus amboinensis*, and concluded that in good recruitment years adult numbers may be limited by density dependant processes, particularly through influences on juvenile growth. In poor recruitment years adult populations reflect variations in recruitment success.

Historically, resource limitation rather than recruitment limitation has been thought to be the main factor structuring coral reef communities, and numerous studies have examined the importance of resource limitation and other post recruitment processes with varying degrees of success. Much of the early work focussed on the assumption of niche diversification, where interspecific competition is assumed to structure the assemblage. However, while many studies documented resource partitioning, few demonstrated any direct evidence of abundance or growth being influenced by resource limitation (Ebeling and Hixon 1991). The first serious challenge to the universality of

the niche diversification hypothesis was made by Sale (1974, 1975, 1977, 1978) and Sale *et al.* (1980) who, in a series of papers, demonstrated that space limitation was the primary factor controlling abundance in a guild of territorial damselfish. It was the availability of space for new recruits to settle into, and chance recruitment into that space, that determined assemblage structure, rather than any post-recruitment competition for resources. Subsequent studies investigating the importance of post-recruitment space limitation have yielded mixed results. For example space limitation in the form of available sleeping holes influences early survivorship of a number of species (Shulman 1984) but not survivorship in adult *Thallasoma bifasciatus* (Robertson and Sheldon 1979).

In more recent years, it has been realised that, at least for some species, competition for food may be equally important as competition for other resources in structuring populations, and that demographic studies should examine differences in growth rate as well as abundance. Jones (1986) and Forrester (1990) have shown that, at least in some species, supplementary feeding can substantially enhance juvenile growth, and Eckert (1985) demonstrated supplementary feeding advances sexual maturity in *Thalassoma lunare* by a year. A number of other studies have shown that intense intraspecific competition can slow growth at higher densities (e.g. Doherty 1982, 1983; Jones 1987a,b; Forrester 1990). This may not be the case at most natural population densities however, as Pitcher (1992) could find no evidence of density dependence in the planktivorous pomacentrid *Pomacentrus nagasakiensis* in either experimental manipulations of abundance, or natural populations. As the experimental densities were an order of magnitude higher than that reported naturally, he concluded individuals of this species would rarely be food limited.

The possibility that growth may be influenced by interspecific competition for food has been investigated in a number of studies. Several of these studies examined the interactions between pairs of ecologically similar species and failed to detect any

influence of competition on growth (Doherty 1982, 1983, 1987; Jones 1987b, 1988). However, a broader examination of possible competitors by Thresher (1983) revealed that growth in the planktivorous *Acanthochromis polyacanthus* was inversely related to the total abundance of all planktivores.

In one of the latest developments in the debate on population regulation in coral reef fishes, predation, particularly on new recruits, has emerged as an alternative process to competition or recruitment limitation. This phenomenon has been reviewed by Hixon (1991). Under the predation hypothesis, predation on fish of all sizes has the potential to reduce population sizes to levels below that at which competition or resource limitation are important. Modelling has shown that small changes in post-recruitment mortality due to factors such as predation can have a significant influence on population structure, by masking or over-riding patterns set by recruitment (Warner and Hughes 1988).

However, very little evidence is yet available to assess the implications of this process due to the difficulties in designing experiments to detect predator impacts.

In the temperate zone, early fisheries-based research indicated that adult fishes normally exist at densities below that at which resources are limited (Cushing 1975). As a consequence of this, and the difficulties of conducting research in cold temperate waters where fish are often hidden amongst the kelp, very little ecological research has focussed on population regulation in temperate reef fishes. A considerable proportion of what research there has been, has concentrated on inter-specific competition in surfperches (e.g. Holbrook and Schmitt 1986, Schmitt and Holbrook 1990). However, surfperches are self-recruiting and as such, would be expected to develop equilibrial populations with the consequent competition for resources, a situation that may not represent that typically found in most reef fishes which have open reproductive systems.

In the remaining temperate studies there is limited evidence, both for and against, the hypothesis that resource limitation is an important factor in population regulation.

Support for resource limitation was given by Thompson and Jones (1983) who found evidence of resource competition between a wrasse and a blenny, Larson (1980) who detected competition between rockfishes, and Jones (1994b) who detected density dependant mortality and growth in the labrid *Pseudolabrus celidotus*.

The studies that present evidence against resource limitation include those of Stephens and Zerba (1981) who discovered little evidence of resource limitation in a temperate reef assemblage, and Norman and Jones (1984) who, using experimental manipulation of food and population abundance, found no evidence of food limitation in the pomacentrid *Parma victoria*. In a more recent study, Francis (1994) could not identify any difference in growth amongst samples of juvenile snapper collected over a 12-18 km spatial scale, suggesting food resources were not a limiting factor in this species.

The emerging picture appears to be that recruitment limitation is likely to be an important factor structuring spatial and temporal variability in reef fish populations, although this structure may also be substantially altered by small changes in post-recruitment mortality *via* mechanisms such as predation (Warner and Hughes 1988). The extent to which recruitment limitation maintains populations below levels where resource limitation becomes an important structuring factor remains unclear. However, it appears that, in high recruitment years, resource limitation may be an important factor, while in poor, and perhaps average recruitment years, recruitment limitation may be the most important factor. The reproductive strategy of each species is also likely to be a critical factor in determining how often recruitment levels are sufficiently high for resource limitation to become important. For example, in live bearing species such as the pomacentrid *Acanthochromis polyacanthus* (Thresher 1983) or the surfperches (Holbrook and Schmitt 1986) where many offspring recruit to the parental reef, recruitment may be sufficiently high that the population is in continuous resource food limitation. The opposite situation may occur in some temperate species that spawn only once per year, and where recruitment is highly variable and depends on factors such as

availability and direction of currents during the larval period. This could lead to a situation where, in the majority of years, recruitment levels are below that at which resource limitation occurs, unless interspecific competition arises due to a strong recruitment of another species which competes for the same resources.

During a series of dives made prior to the beginning of this study, I observed that isolated populations of a number of the species included in the present investigation appeared to have considerably different size structures and, in the case of sex inverting species, different size at sex inversion. These observations suggested that growth rates may differ between populations, even amongst those sharing similar habitats and environmental conditions, and that they possibly represented a mosaic of populations experiencing different levels of resource limitation, presumably food limitation. These observations appeared to run counter to the central assumptions of the open, non-equilibrial models of population and community regulation in reef fishes.

The aim of the research presented in this chapter was to test the validity of the open, non-equilibrial models by examining and comparing growth rates and growth curves from a number of populations occupying similar habitats for evidence of resource limitation. Differences in the elevation of growth curves should indicate differences in early juvenile growth rates (assuming similar timing of recruitment), and differences in slopes of the growth curves should indicate differing growth rates in adult as well as juvenile populations. I chose to work with six of the most common reef fishes found in Tasmanian waters so that any findings would form the basis of a broadly applicable model. These species were the labrids *Notolabrus tetricus*, *Notolabrus fucicola*, *Pictilabrus laticlavius*, and *Pseudolabrus psittaculus*, and the monacanthids *Penicipelta vittiger* and *Meuschenia australis*.

## 6.2 Materials and methods.

### 6.2.1 Species and Collections

The species collected were the labrids *Notolabrus tetricus*, *Notolabrus fucicola*, *Pictilabrus laticlavius*, and *Pseudolabrus psittaculus*, and the monacanthids *Penicipelta vittiger* and *Meuschenia australis*, all of which are permanent reef residents (Chapter 2). As movement in all of these species was shown to be restricted by natural habitat boundaries (Chapter 2), the collection sites were chosen such that they were separated from each other by at least a 1 km wide habitat barrier, to ensure each sampled population was independent of any other.

Fish collections were made at several times and different locations during this study, primarily because not all sites within one location yielded enough individuals for proper analysis. An initial collection was made in the Huon region in April/May 1993. The sites included at this location were Roaring Beach, Butts Reef, and Charlotte Cove (Fig. 2.1) and were subject to similar exposure to wave action (light to moderate), and under the influence of the tannin rich discharge waters of the Huon River.

As *N. tetricus* was the only species collected in sufficient numbers in the Huon region collection, a further collection was carried out at Piersons Point, near Tinderbox, and at One Tree Point on Bruny Island (Fig. 4.1), two sites sharing a similar habitat on the exposed coast south of Hobart, in July/August 1993, in order to collect a wider range of species. Unfortunately, despite a substantial effort, insufficient numbers of all species except *N. tetricus* were collected for proper analysis. The final collection was made at five locations with ecologically similar habitats on the Tasmanian East Coast, in February/March 1994 (Fig. 6.1). These sites were at Garden Point and Stinking Bay in Port Arthur, and at Fortescue Bay, Marion Bay, and Spring Beach. They were characterised as sites with moderate exposure to swells, under strong oceanic influence.



### 6.2.2 Collection methods and procedures

Fish were collected using fish traps, fine mesh nets, and by spearing, and every effort was made to ensure as wide a range of size classes as possible was collected, including juveniles. For the two monacanthid species, sufficient numbers of both males and females had to be collected from each site, as growth is significantly different between sexes (Chapter 4), and therefore the sexes must be analysed separately. For the remaining species, both sexes could be pooled for analysis, as growth of males and females is similar in *N. fucicola*, and in the protogynous hermaphrodites, *N. tetricus*, *P. laticlavius*, and *P. psittaculus*, male growth is simply a continuation of female growth (Chapter 4). Captured fish were kept on ice until they were processed. Measurements were made of total length, total weight, and gonad weight. Sexes were determined from body morphology and coloration, and from inspection of gonads. The otoliths were removed and dried. The age of each fish was determined from counts of otolith annuli, using the methods described and validated in Chapter 3.

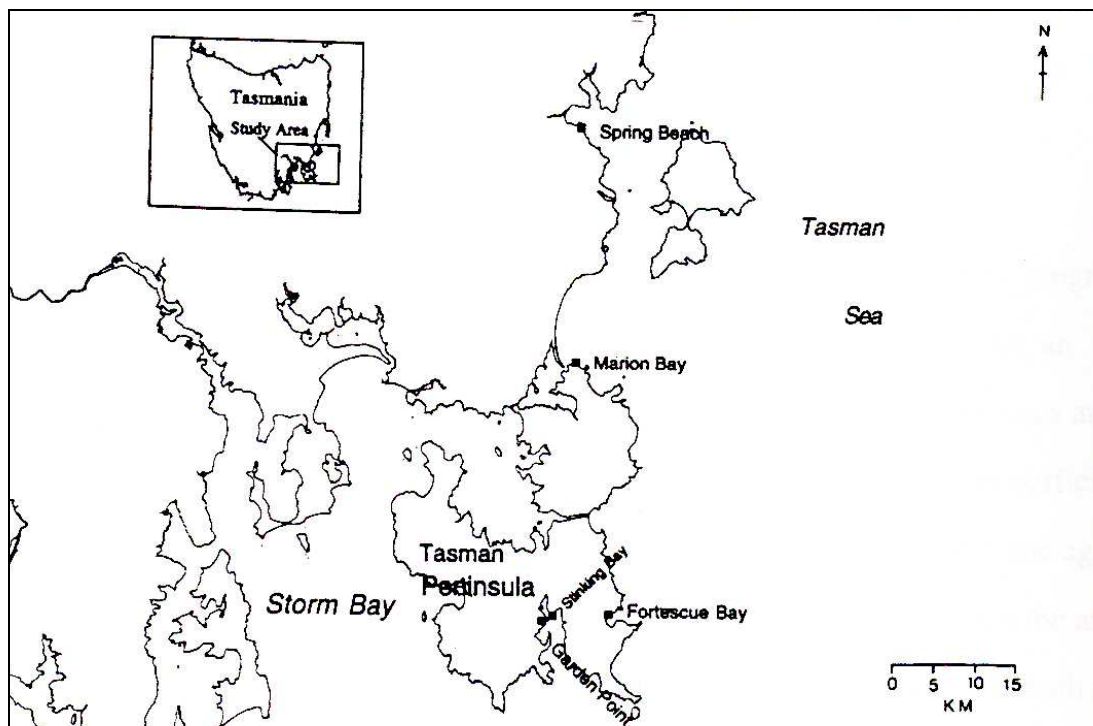


Figure 6.1 Sites on the Tasmanian East Coast at which fish collections were made in February and March 1994.

### 6.2.3 Analysis

As the aim of this research was to investigate any differences in the growth rate of populations of reef fishes occupying similar habitats under similar environmental conditions, growth was compared between populations using the ANOVA method of Haskard (1992), on the length at age data. With this method, a difference in growth between populations will generally produce a significant age by population interaction, which can be partitioned into linear, quadratic, and higher order components to indicate the shape of differences. While this method potentially lacks power by not assuming that the growth curves have a specific shape, it avoids the errors inherent in non-linear estimation of parameters such as  $K$  and  $L_{\infty}$ , parameters that are often used in the comparison of growth between populations. By ignoring the fit to a specific shape, this method may actually gain some power, as not all growth curves obtained from population samples are simple. Some cohorts may grow faster (at least initially) than others, resulting in an irregular growth curve, and one that may differ between populations, even though the overall "mean" curve may be similar. The ANOVA method of Haskard (1992) will detect such irregularities if they differ between populations, as they will show as an interaction term  $\text{site} \times \text{age}$ .

The ANOVA's were calculated using the MGLH function of the computer program SYSTAT, which uses a type III sum of squares approach in its calculations, an approach suited to the unbalanced data sets used. Not all size classes and sites are included in each analysis, however, as some species were not collected in sufficient numbers at all sites, and for most species, significant differences between the age class structure of each site meant that many age classes had to be removed from the analysis. This presented problems for analysis of *P. psittaculus*, *P. laticlavus*, and both male and female *M. australis* from the East Coast survey, as substantial between population differences in the age structures of fish collected, meant that most of the data would have to be ignored. Therefore, inter-population differences in growth were examined in these species using ANCOVA, allowing most age classes to be used in the calculations,

but losing some of the power of the ANOVA method. In all cases, untransformed data was used as no transformation was found that could improve the distribution of residuals. In species whose growth was analysed by ANCOVA, age classes at the extremes of the growth curve were removed from the analysis if they were shown to provide excessive shape to residual plots.

As well as comparison of sites within each location, the influence of different environmental conditions on growth was also examined. This was achieved by comparing growth from the East Coast with that from the Huon region. As a difference of two months existed between the timing of the two collections, individuals of the same age from the Huon region had a two month growth advantage over those from the East Coast. It was not possible to adjust the data for this, when using the ANOVA method of Haskard (1992). However, this is not a problem if this difference is taken into account in interpreting the results. A difference in collection timing will not alter the relationship between the shapes of the growth curves compared, it will only influence elevation. Any detected difference in elevation can then be interpreted in the light of known differences in the timing of the collections, i.e. is this difference equivalent in magnitude and direction to two months growth, or is it necessary to invoke another cause ?

### **6.3 Results**

#### *6.3.1 Variation in growth between sites with similar habitats*

*6.3.1.1 Notolabrus tetricus:* Sufficient numbers of *N. tetricus* individuals were collected to allow for comparison of growth between populations occupying similar habitats in all three surveys. In the first survey (Huon region) growth was compared between the Charlotte Cove and Butts Reef sites (Table 6.1) In the second survey, growth was compared between Piersons Point at Tinderbox, and One Tree Point on Bruny Island (Table 6.2a), and in the third survey (East Coast survey) growth was compared between all five sites at which collections were made (Table 6.3a). No significant differences in

growth were detected in any of the population comparisons made using two-factor ANOVA, either in curve elevation (B,  $p = 0.92$ ,  $0.79$ , and  $.011$  respectively), the shape term ( $A*B$ ,  $p = 0.87$ ,  $0.87$ , and  $0.25$  respectively) or higher order interaction terms (examined, but not shown in the tables). While the mean length at age for each age class did differ between the sites compared, it rarely exceeded 1.5 cm in age classes represented by at least three replicates, a length equivalent to approximately half a years growth (Chapter 3). As growth was similar at all sites on the East Coast, the length at age data for these sites was pooled to produce a growth relationship for *N. tetricus* on the East Coast (Fig. 6.2). The von Bertalanffy growth curve was fitted to these data using the methods described in Chapter 3, and the estimated von Bertalanffy parameters were,  $L_{\infty} = 51.27$ ,  $K = 0.111$ ,  $T_0 = -1.35$ .

Table 6.1 (a) Two-factor ANOVA comparing the length at age relationships of *N. tetricus* at two ecologically similar sites (Charlotte Cove and Butts Reef) in the Huon Region in April/May 1993. The age classes included are 3+, 4+, and 9+. ( $n = 48$ )

Source	d.f	s.s	m.s.	F	P
Age (A)	2	547.6	273.8	107.4	<0.001
Site (B)	1	0.023	0.023	0.009	0.919
A*B	2	0.664	0.332	0.133	0.868
Error	42	107.0	2.552		

(b) Mean length (in cm), and number of individuals collected (n), at each site and in each age class used in the ANOVA.

Site	Age Class		
	3+	4+	9+
Butts Reef	19.3 (6)	21.7 (22)	29.7 (6)
Charlotte Cove	19.0 (3)	21.7 (8)	30.2 (3)

Table 6.2 (a) Two-factor ANOVA comparing the length at age relationships of *N. tetricus* at two ecologically similar sites (Piersons Pt and One Tree Pt) in the Tinderbox Region in July/Aug 1993. The age classes included are 3<sup>+</sup>, 4<sup>+</sup>, and 5<sup>+</sup>. (n = 46)

Source	d.f.	s.s	m.s.	F	P
Age (A)	2	261.8	130.9	54.71	<0.001
Site (B)	1	0.171	0.167	0.714	0.792
A*B	2	0.692	0.343	0.138	0.874
Error	40	95.67	2.391		

(b) Mean length (in cm), and number of individuals collected (n), at each site and in each age class used in the ANOVA.

Site	Age Class		
	3+	4+	5+
Piersons Pt	19.4 (15)	21.6 (7)	25.1 (9)
One Tree Pt	19.2 (7)	22.0 (3)	25.2 (5)

Table 6.3 (a) Two-factor ANOVA comparing the length at age relationships of *N. tetricus* at five sites on the Tasmanian East Coast in Feb/Mar 1994. The age classes included are 3<sup>+</sup>, 4<sup>+</sup>, 5<sup>+</sup> and 6<sup>+</sup>. (n = 145)

Source	d.f	s.s	m.s.	F	P
Age (A)	3	844.4	281.9	109.4	<0.001
Site (B)	4	19.73	4.932	1.903	0.113
A*B	12	39.03	3.248	1.258	0.253
Error	125	324.2	2.591		

(b) Mean length (in cm), and number of individuals collected (n), at each site and in each age class used in the ANOVA.

Site	Age Class			
	3+	4+	5+	6+
Garden Pt	20.9 (16)	23.1 (10)	27.7 (19)	29.0 (4)
Stinking Bay	21.0 (8)	23.5 (7)	27.1 (2)	27.9 (2)
Fortescue Bay	20.1 (15)	22.9 (9)	27.7 (6)	30.1 (1)
Marion Bay	21.6 (11)	26.5 (1)	28.0 (3)	30.3 (2)
Spring Beach	22.9 (11)	24.4 (13)	26.8 (4)	29.3 (1)

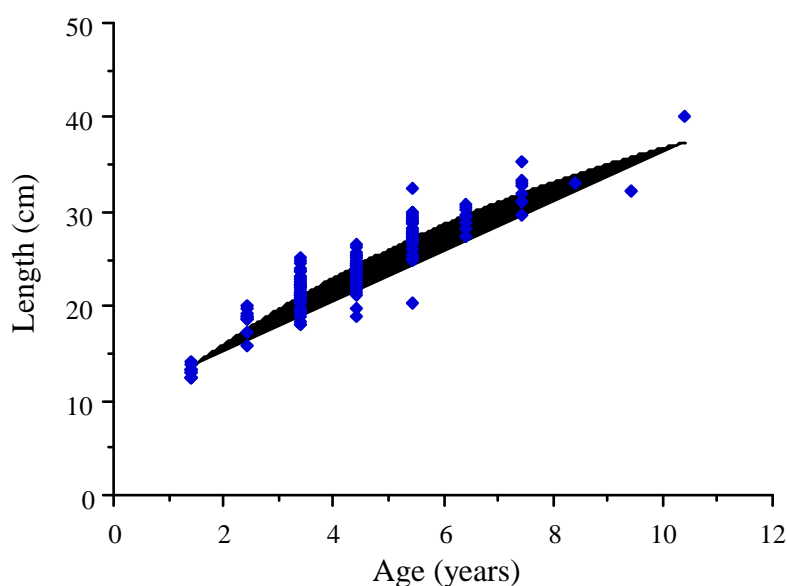


Figure 6.2 Length at age relationship of *Notolabrus tetricus* collected from the Tasmanian East Coast in Feb/March 1993, and fitted with a von Bertalanffy growth curve calculated from those data.

6.3.1.2 *Notolabrus fucicola*: This species was only collected in sufficient numbers from the East Coast collection to allow for population growth comparisons to be made.

Comparisons were made between four of the East Coast sites, excluding Stinking Bay.

No significant differences in growth were found between the sites when examined by two-factor ANOVA (Table 6.4a), either in elevation (B,  $p = 0.15$ ) or shape ( $A*B$ ,  $p = 0.14$ ). As growth was similar at all sites on the East Coast, the length at age data for these sites was pooled to produce a growth relationship for *N. fucicola* on the East

Coast (Fig. 6.3). The von Bertalanffy growth curve was fitted to these data using the methods described in Chapter 3, and the estimated von Bertalanffy parameters were,  $L_{\infty} = 43.38$ ,  $K = 0.113$ ,  $T_0 = -1.64$ .

Table 6.4 (a) Two-factor ANOVA comparing the length at age relationships of *N. fucicola* at four sites on the Tasmanian East Coast (Garden Pt, Fortescue Bay, Marion Bay, and Orford) in Feb/Mar 1994. The age classes included are 1+, 2+, 3+, 4+ and 5+. (n= 95)

Source	d.f.	s.s	m.s.	F	P
Age (A)	4	1467	366	133	<0.001
Site (B)	3	15.25	5.08	1.82	0.152
AB	12	50.92	4.24	1.52	0.138
Error	75	209.2	2.79		

(b) Mean length (in cm), and number of individuals collected (n), at each site and in each age class used in the ANOVA.

Site	Age Class				
	1+	2+	3+	4+	5+
Garden Pt	12.1 (4)	14.0 (3)	18.7 (4)	21.8 (5)	25.6 (4)
Fortescue Bay	13.5 (4)	17.1 (1)	20.8 (16)	20.6 (8)	24.1 (4)
Marion Bay	11.2 (5)	15.3 (3)	18.6 (5)	21.2 (3)	23.1 (8)
Spring Beach	12.9 (5)	13.6 (2)	19.3 (2)	21.4 (7)	24.0 (5)

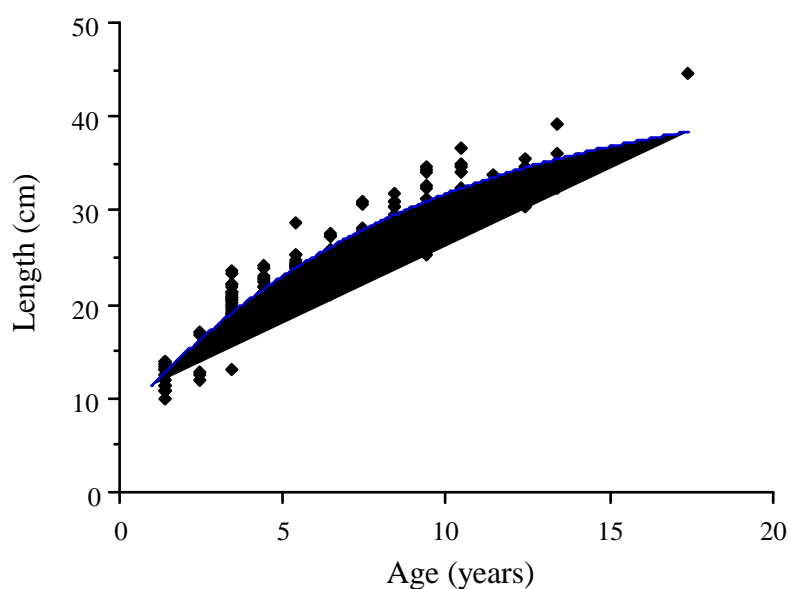


Figure 6.3 Length at age relationship of *Notolabrus fucicola* collected from the Tasmanian East Coast in Feb/March 1993, and fitted with a von Bertalanffy growth curve calculated from those data.

6.3.1.3 *Pictilabrus laticlavius* and *Pseudolabrus psittaculus*: Sufficient numbers of individuals of both species were obtained in the East Coast collection to allow for comparison of growth between populations at four of the five sites, excluding Stinking Bay. Comparison of fish growth by ANCOVA (Tables 6.5 & 6.6) found that for both species, there was no significant difference in growth between sites, in either elevation (B, for *P. laticlavius*  $p = 0.33$ , for *P. psittaculus*  $p = 0.96$ ), or slope (A\*B, for *P. laticlavius*  $p = 0.14$ , for *P. psittaculus*  $p = 0.77$ ). The East Coast growth curves of these species are shown in Chapter 3.

Table 6.5 A comparison of the growth of *Pictilabrus laticlavius* at five sites on the Tasmanian East Coast (Garden Pt, Stinking Bay, Fortescue Bay, Marion Bay, and Orford) in Feb/Mar 1994 using ANCOVA. (n = 41)

Source	d.f.	s.s	m.s.	F	P
Age (A)	1	20.2	20.2	10.8	0.003
Site (B)	4	9.12	2.28	1.22	0.333
A*B	4	13.9	3.48	1.85	0.141
Error	31	58.1	1.88		

Table 6.6 A comparison of growth of *Pseudolabrus psittaculus* at four sites on the Tasmanian East Coast (Garden Pt, Fortescue Bay, Marion Bay, and Orford) in Feb/Mar 1994 using ANCOVA. (n = 43).

Source	d.f.	s.s	m.s.	F	P
Age (A)	1	27.5	27.5	11.9	0.001
Site (B)	3	0.68	0.23	0.10	0.963
A*B	3	2.63	0.88	0.38	0.769
Error	35	80.8	2.31		

6.3.1.4 *Penicipelta vittiger*: Sufficient individuals of this species were obtained in the East Coast collection to allow for a comparison of growth differences between populations using two-factor ANOVA. As growth was shown to differ significantly between the sexes of this species in Chapter 3, each sex was considered separately. In both cases no significant differences were found in growth between the sites compared



(Tables 6.7a & 6.8a) in either elevation (B, for females  $p = 0.56$ , for males  $p = 0.33$ ) or shape (A\*B, for females  $p = 0.79$ , for males  $p = 0.52$ ).

Table 6.7 (a) Two-factor ANOVA comparing the length at age relationships of *Penicipelta vittiger* females at four sites on the Tasmanian East Coast (Garden Pt, Fortescue Bay, Marion Bay, and Orford) in Feb/Mar 1994. The age classes included are 1<sup>+</sup>, and 2<sup>+</sup>. (n = 62).

Source	d.f	s.s	m.s	F	P
Age (A)	1	416	416	121	<0.001
Site (B)	3	7.06	2.36	0.69	0.563
A*B	3	3.55	1.18	0.35	0.792
Error	54	185	3.43		

(b) Mean length (in cm), and number of individuals collected (n), at each site and in each age class used in the ANOVA.

Age Class	Site			
	Garden Pt	Fortescue Bay	Marion Bay	Orford
1+	18.6 (9)	19.0 (4)	18.9 (8)	17.8 (16)
2+	25.0 (9)	24.7 (3)	24.2 (9)	24.0 (4)

Table 6.8 (a) Two-factor ANOVA comparing the length at age relationships of *Penicipelta vittiger* males at four sites on the Tasmanian East Coast (Garden Pt, Fortescue Bay, Marion Bay, and Orford) in Feb/Mar 1994. The age classes included are 1<sup>+</sup>, and 2<sup>+</sup>. (n = 62).

Source	d.f	s.s	m.s	F	P
Age (A)	1	703	703	327	<0.001
Site (B)	3	7.62	2.53	1.17	0.329
A*B	3	17.7	5.91	2.74	0.523
Error	57	123	2.15		

(b) Mean length (in cm), and number of individuals collected (n), at each site and in each age class used in the ANOVA.

Age Class	Site			
	Garden Pt	Fortescue Bay	Marion Bay	Orford
1+	17.9 (2)	17.7 (9)	18.7 (4)	19.4 (4)
2+	26.3 (10)	25.4 (13)	26.2 (14)	27.9 (9)

As growth was similar at all sites on the East Coast, the length at age data for these sites was pooled to produce a growth relationship for *P. vittiger* females on the East Coast (Fig. 6.4). The von Bertalanffy growth curve was fitted to these data using the methods described in Chapter 3, and the estimated von Bertalanffy parameters were,  $L_{\infty} = 25.16$ ,  $K = 2.930$ ,  $T_0 = 0.97$ . The East Coast growth curve for males of this species is shown in Chapter 3.

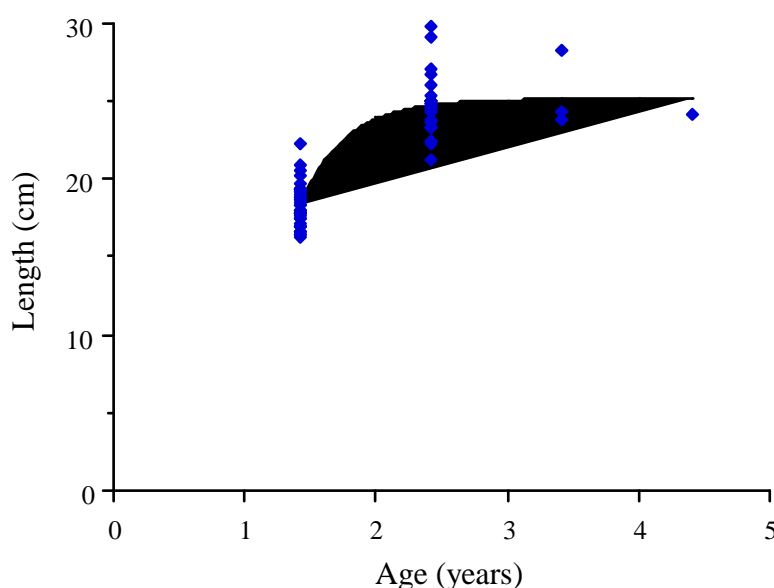


Figure 6.4 Length at age relationship of *Penicipelta vittiger* females collected from the Tasmanian east coast in Feb/March 1993, and fitted with a von Bertalanffy growth curve calculated from those data.

6.3.1.5 *Meuschenia australis*: This species was not abundant at the East Coast sites at which collections were made. However, sufficient numbers were obtained to allow for a limited analysis of growth rates between populations. This analysis was restricted by the need to consider male and female growth separately, as their growth rates are different (Chapter 3). It was further limited by a lack of common age classes at the sites examined. Therefore for both sexes, growth between sites where sufficient individuals were present, was compared by ANCOVA. For both sexes the sites compared were Garden Point, Fortescue Bay, and Marion Bay, and Spring Beach.

Table 6.7 (a) Two-factor ANOVA comparing the length at age relationships of *Penicipelta vittiger* females at four sites on the Tasmanian East Coast (Garden Pt, Fortescue Bay, Marion Bay, and Orford) in Feb/Mar 1994. The age classes included are 1<sup>+</sup>, and 2<sup>+</sup>. (n = 62).

Source	d.f	s.s	m.s	F	P
Age (A)	1	416	416	121	<0.001
Site (B)	3	7.06	2.36	0.69	0.563
A*B	3	3.55	1.18	0.35	0.792
Error	54	185	3.43		

(b) Mean length (in cm), and number of individuals collected (n), at each site and in each age class used in the ANOVA.

Age Class	Site			
	Garden Pt	Fortescue Bay	Marion Bay	Orford
1+	18.6 (9)	19.0 (4)	18.9 (8)	17.8 (16)
2+	25.0 (9)	24.7 (3)	24.2 (9)	24.0 (4)

Table 6.8 (a) Two-factor ANOVA comparing the length at age relationships of *Penicipelta vittiger* males at four sites on the Tasmanian East Coast (Garden Pt, Fortescue Bay, Marion Bay, and Orford) in Feb/Mar 1994. The age classes included are 1<sup>+</sup>, and 2<sup>+</sup>. (n = 62).

Source	d.f	s.s	m.s	F	P
Age (A)	1	703	703	327	<0.001
Site (B)	3	7.62	2.53	1.17	0.329
A*B	3	17.7	5.91	2.74	0.523
Error	57	123	2.15		

(b) Mean length (in cm), and number of individuals collected (n), at each site and in each age class used in the ANOVA.

Age Class	Site			
	Garden Pt	Fortescue Bay	Marion Bay	Orford
1+	17.9 (2)	17.7 (9)	18.7 (4)	19.4 (4)
2+	26.3 (10)	25.4 (13)	26.2 (14)	27.9 (9)

No significant site related differences in growth were found in either sex (Tables 6.9 & 6.10) in either elevation (B,  $p = 0.58$  for females and  $0.20$  for males) or slope ( $A*B$ ,  $p = 0.67$  for females and  $0.25$  for males). As growth was found to be similar at all sites on the East Coast, the length at age data for these sites was pooled to produce a growth relationship for *M. australis* females on the East Coast (Fig. 6.5). The von Bertalanffy growth curve was fitted to this data using the methods described in Chapter 3, and the estimated von Bertalanffy parameters were,  $L_{\infty} = 29.78$ ,  $K = 0.113$ ,  $T_0 = -2.85$ . The East Coast growth curve for males of this species is shown in Chapter 3.

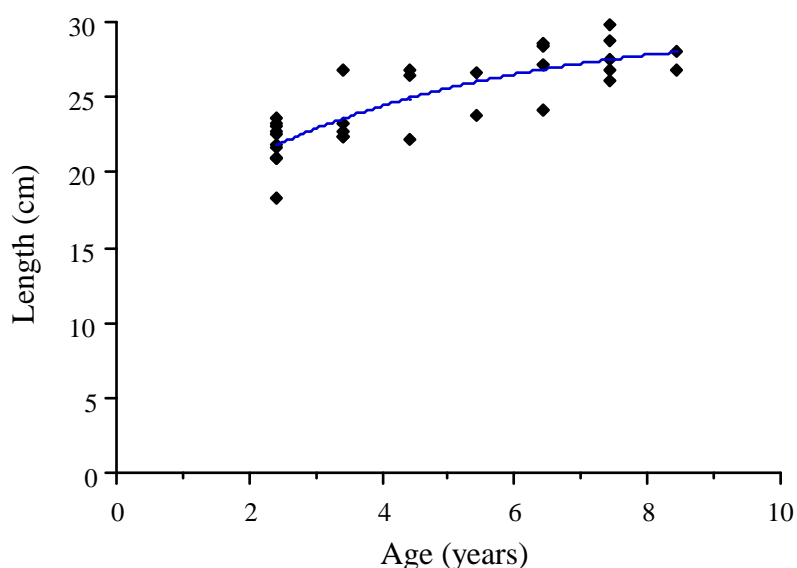


Figure 6.5 Length at age relationship of *Meuschenia australis* females collected from the Tasmanian East Coast in Feb/March 1993, and fitted with a von Bertalanffy growth curve calculated from those data.

### 6.3.2 Variation in growth between habitats

6.3.2.1 *Notolabrus tetricus*: A two-way ANOVA comparing the length at age relationship of *N. tetricus* from the East Coast collection with that from the Huon collection (Table 6.11), found habitat differences (B) to be significant ( $p = 0.0001$ ), although the interaction term ( $A*B$ ) was not significant ( $p = 0.96$ ). This result suggests that there is an elevation difference in the growth curves between the different habitats, but not one in shape, and as this elevation difference is due to the East Coast length at

age mean being consistently higher than those from the Huon region (Table 6.11b), it is a real effect rather than just one due to the difference in timing of the surveys.

Table 6.11 (a) Two-factor ANOVA comparing the length at age relationships of *Notolabrus tetricus* from the East Coast collection with that from the Huon collection. (n = 178)

Source	d.f	s.s	m.s	F	P
Age (A)	3	2092	697	327	<0.001
Site (B)	1	91.4	91.4	42.9	<0.001
A*B	3	0.67	0.23	0.11	0.958
Error	170	362	2.13		

(b) Mean length (in cm), and number of individuals collected (N), in each age class used in the ANOVA.

Location	Age Class			
	1+	2+	3+	4+
Huon	11.1 (16)	16.0 (3)	19.2 (9)	21.7 (30)
East Coast	13.1 (10)	18.5 (9)	21.2 (61)	23.7 (40)

6.3.2.2 *Notolabrus fucicola*: A two-factor ANOVA (Table 6.12a), comparing growth in *N. fucicola* from the East Coast with those from the Huon region found growth between these habitats (B) to be significantly different ( $p = 0.011$ ), although the interaction term (A\*B) was not significant ( $p = 0.55$ ), suggesting the difference in growth curves is due to elevation rather than shape. As in *N. tetricus*, the elevation difference appears to be due to the East Coast length at age means being consistently higher than those from the Huon region (Table 6.12b), and thereby constituting a real effect rather than one related to survey timing.

Table 6.12 (a) Two-factor ANOVA comparing the length at age relationship of *Notolabrus fucicola* from the East Coast collection with that from the Huon collection. (n = 202)

Source	d.f	s.s	m.s	F	P
Age (A)	10	717	71.7	206	<0.001
Site (B)	1	22.6	22.6	6.48	<0.001
A*B	10	29.5	2.95	0.85	0.553
Error	180	626	3.48		

(b) Mean length (in cm), and number of individuals collected (n), in each age class used in the ANOVA.

Age Class	Location	
	Huon	East Coast
1+	11.5 (19)	12.3 (18)
2+	15.8 (3)	14.7 (9)
3+	19.5 (4)	19.9 (28)
4+	21.5 (2)	21.2 (23)
5+	23.2 (4)	24.1 (8)
6+	22.8 (3)	25.2 (8)
7+	27.6 (2)	27.7 (19)
8+	27.5 (2)	29.7 (10)
9+	28.9 (8)	30.8 (11)
10+	30.1 (3)	32.2 (12)
11+	31.5 (2)	32.2 (3)

6.3.2.3 *Pictilabrus laticlavius*: For this species the growth relationships from the East Coast collection and Huon collection were compared by ANCOVA (Table 3.4) and no significant differences in growth were detected in either the site ( $p = 1.00$ ) or the interaction term ( $p = 0.86$ ). These results suggest that growth is similar in both locations.

6.3.2.4 *Pseudolabrus psittaculus*: A comparison of East Coast fish growth with that from the Huon region by two-factor ANOVA (Table 6.13a), demonstrated growth is significantly different between the two habitats (B,  $p = 0.018$ ) although the interaction

term (A\*B) is not significant ( $p = 0.15$ ), suggesting that the difference in growth curves is due to elevation only, and that this elevation difference is a real effect, with the mean lengths at age from the Huon region being consistently lower than those from the East Coast (Table 6.13b).

Table 6.13 (a) Two-factor ANOVA comparing the length at age relationship of *Pseudolabrus psittaculus* from the East Coast collection with that from the Huon collection. (n = 39)

Source	d.f	s.s	m.s	F	P
Age (A)	3	490	163	113	<0.001
Site (B)	1	9.00	9.00	6.24	0.018
A*B	3	8.18	2.73	1.89	0.152
Error	31	44.7	1.44		

(b) Mean length (in cm), and number of individuals collected (n), in each age class used in the ANOVA.

Location	Age Class			
	1+	2+	3+	4+
Huon	11.7 (8)	11.0 (1)	17.6 (2)	19.4 (8)
East Coast	12.0 (6)	14.7 (4)	18.2 (2)	19.9 (8)

6.3.2.5 *Penicipelta vittiger*: Few male *P. vittiger* were collected in the Huon region, and comparisons of growth for this sex between the Huon region and the East Coast was restricted to a t-test of the means of the 2+ age class (shown in Chapter 3), which indicated that growth is not significantly different between the two different habitats ( $p = 0.09$ ). For females, more individuals and age classes were collected, allowing for a comparison of growth by two-factor ANOVA (Table 6.14a). This indicated that there is no significant difference in growth between the two habitats either in elevation (B,  $p = 0.18$ ) or shape (A\*B,  $p = 0.17$ ).

Table 6.14 (a) Two-factor ANOVA comparing the length at age relationship of *Penicipelta vittiger* females from the East Coast collection with that from the Huon collection. (n = 77)

Source	d.f	s.s	m.s	F	P
Age (A)	1	529	529	150	<0.001
Site (B)	1	6.43	6.43	1.83	0.182
AB	1	6.63	6.63	1.88	0.169
Error	73	256	3.52		

(b) Mean length (in cm), and number of individuals collected (n), in each age class used in the ANOVA.

Location	Age Class	
	1+	2+
Huon	18.3 (10)	26.1 (5)
East Coast	18.3 (37)	24.5 (9)

6.3.2.6 *Meuschenia australis*: For males, differences in growth between the East Coast and the Huon region were compared by ANCOVA in Chapter 3, and a significant difference in growth was detected in both the site term ( $p < 0.001$ ) and the interaction term ( $p < 0.001$ ), suggesting that growth is faster at the East Coast sites. For females, growth rate differences were compared by two-factor ANOVA (Table 6.14a), which indicated that there is no significant difference in growth between the two different habitat types, either in elevation (B,  $p = 0.92$ ) or slope (A\*B,  $p = 0.51$ ).

## 6.4 Discussion.

### 6.4.1 Growth in similar habitats

In each of the six species included in this study, no significant difference in growth was detected between populations occupying similar habitats, either in the shape of the growth curves (in species analysed by ANOVA), or in their slope (species analysed by ANCOVA). It is possible that this result may be due to a lack of power in the tests used, arising from the small number of replicates available at some of the sites and age



Table 6.15 (a) Two-factor ANOVA comparing the length at age relationship of *Meuschenia australis* females from the East Coast collection with that from the Huon collection. (n = 48)

Source	d.f	s.s	m.s	F	P
Age (A)	6	236	39.4	11.2	<0.001
Site (B)	1	0.03	0.03	0.01	0.923
A*B	6	18.7	3.11	0.89	0.512
Error	34	119	3.49		

(b) Mean length (in cm), and number of individuals collected (n), in each age class used in the ANOVA.

Age Class	Location	
	Huon	East Coast
2+	21.0 (4)	21.8 (11)
3+	25.8 (1)	23.5 (5)
4+	22.9 (2)	25.2 (3)
5+	24.6 (4)	25.2 (2)
6+	27.4 (1)	27.1 (4)
7+	26.4 (2)	27.8 (5)
8+	29.4 (2)	27.4 (2)

classes compared. However, a comparison of mean lengths at age between populations in the species compared by ANOVA (*Notolabrus tetricus*, *Notolabrus fucicola*, and *Penicipelta vittiger*) shows that even after 4-5 years of growth in the labrids and 2 years of growth in the monacanthid, population means differ by less than a few months growth. Therefore, even if type II errors were made, and population differences do exist, they must be small, and future experiments attempting to examine the magnitude of this difference will need to take this into account. Sampling strategies in future investigations should concentrate on obtaining sufficient replicates in the early age classes of long-lived species such as the labrids investigated here, as they are generally more abundant than older age classes. There is also less chance of obtaining samples where one population sample may be dominated by an age not present in others.

As well as no difference being found between the shape or slope of the growth curves in the species investigated, no difference in elevation was detected either. Because elevation effects would have been due to consistent site differences in either the timing of recruitment, or early juvenile growth, it appears that neither of these factors varied amongst the populations sampled.

It would have been preferable, and perhaps far more informative, to examine growth between populations on a cohort (age class) basis rather than just examining a population average. This would have yielded valuable information on the spatial and temporal nature of growth variation, information which is restricted in a snapshot survey such as this one. Unfortunately, as the growth of otoliths is not in one plane for the labrid fishes examined here, it was not possible to back-calculate the length at age relationship of individual fish, and to develop growth curves for each cohort. Future work examining growth at the population level in temperate fishes should concentrate on species where back calculation of individual growth trajectories is possible, as several recent studies such as those of Boehlert *et al.* (1989) on commercial open water species, and Pitcher (1992) on juvenile growth in a tropical pomacentrid, have shown this method to be particularly useful.

#### 6.4.2 *Growth in different habitats*

The influence of habitat on growth differs by species. For *Pictilabrus laticlavus*, *Penicipelta vittiger* and females of *Meuschenia australis*, the two habitats (slight to moderately exposed, river influenced and moderately exposed, open coastal), and habitat related factors, were not sufficiently different to influence growth. However, significant differences in the elevation of growth curves were detected in *Notolabrus tetricus*, *Notolabrus fucicola*, and *Pseudolabrus psittaculus*, and a significant difference in the slope of the growth curve was detected in males of *Meuschenia australis*. For *M. australis* males, overall growth appeared to be greater at the East Coast sites than at the Huon sites. It appears somewhat incongruous, however, that females of this species

grew at similar rates in both habitats, suggesting that the low number of replicates available for comparison of growth in male *M. australis* may have lead to a type I error.

In the remaining species (*N. tetricus*, *N. fucicola* and *Pseudolabrus psittaculus*) the difference in the elevation of the growth curves indicated that for any given age, individuals from the Huon region were smaller than those from the East Coast sites. Although this difference in elevation must be due to either differences in the timing of recruitment or the magnitude of early juvenile growth between habitats, it is not possible, from the present data, to isolate which of these two factors is most important in explaining this difference. Certainly habitat related differences in juvenile growth are a distinct possibility, and may be a common feature of growth in juvenile reef fishes. However, few studies have attempted to document this, or the factors causing such growth variation. In one of the few studies to date, Sogard (1992) found growth in juveniles of three temperate fishes to vary between habitats within an estuary, and suggested that differences in water temperature, sediment structure, and food availability may have been the factors influencing growth variation.

Most studies examining habitat related differences in growth of fishes have concentrated on freshwater systems, where the degree of risk of predation has been shown to substantially influence feeding strategies, including habitat preference (e.g. Milinski and Heller 1978; Werner *et al.* 1983). In the study by Werner *et al.* (1983) the threat of predation was shown to be an important factor influencing growth in the bluegill sunfish, *Lepomis macrochiris*, suggesting that growth may be influenced by the ratio of food to available shelter in each habitat. Predation has also been shown to be an important influence on foraging behavior in a marine fish. Holbrook and Schmitt (1985, 1988a, 1988b) found predation risk to influence habitat choice in the surfperch *Embiotoca jacksonii*, and that feeding rates were lower when predators were present.

#### 6.4.3 General discussion

For the six temperate reef fishes investigated in this study, growth curves appear to be remarkably similar in populations occupying ecologically equivalent habitats, although, at least in some species, habitat differences were shown to have an influence on growth. For the species where growth was compared by ANOVA, not only did populations in equivalent habitats have similar growth, but no significant year by site interactions were found, suggesting that growth in each particular year class was similar across the populations surveyed. These results suggest that, at least for the species investigated here, population growth is best explained by open, non-equilibrial models such as those of Doherty and Williams (1988a, 1988b) or Hixon (1991). These models suggest that either recruitment levels are usually sufficiently low, or post-recruitment mortality is usually sufficiently high, that populations are not resource limited, at least for resources which may influence growth.

Several other studies examining growth in reef associated fishes have also found little variation in growth between similar habitats, including the temperate studies of Francis (1994) on juvenile snapper (*Pagrus auratus*), Norman and Jones (1984) on the pomacentrid *Parma victoria*, and a study of growth in juveniles of the tropical pomacentrid *Pomacentrus nagasakiensis* by Pitcher (1992). These are in addition to a study examining resource availability in a community of temperate reef fishes which found neither food nor space were limiting factors (Stephens and Zerba 1981). There are, however, a number of other studies demonstrating an inverse relationship between population density and growth (e.g. Jones 1984b, 1990; Forrester 1990) which suggest that not all species are free from resource competition. One of these studies (Jones 1984b) was on the temperate labrid *Notolabrus celidotus*, a species closely related to several of the labrids in this study. While Jones found that juvenile growth was inversely related to density, a variety of habitats were censused in his study, and habitat effects and density effects on growth were not partitioned, leaving some doubt as to which factor was primarily responsible for the observed variation in growth.

Assuming that growth in some populations of *N. celidotus* was limited by resource availability rather than environmental factors, it appears from the available evidence that in temperate reef systems, not all populations in all species are free from resource limitation all of the time, and therefore no single population model is likely to be exclusive. A similar conclusion was reached by Ebeling and Hixon (1991) who stated "all (population) models may operate to greater or lesser extents in temperate and tropical systems, depending on local environmental conditions during the study and during the system's recent history. Any search for "the factor" regulating reef fish community structure is thus doomed to failure and sweeping generalisations should be suspect.....There may always be more than one structuring process and these processes may change in relative importance from place to place and through time".

While it appears that for the six temperate reef species included in this study, open non-equilibrium models may apply most of the time, it is likely that at least occasionally resource limitation (for factors influencing growth) must occur. The question still remains then, as to exactly how often natural populations in most of these, and other temperate species, do experience resource limitation during part, or all of their post recruitment growth, and to what extent reproductive strategies play a role in this process.

The answer to the first question may be found by examining growth in species of fish in which back-calculation of growth rates of individual fish to the time of settlement is simple and reliable. By collecting sufficient replicates in each available age class, at several locations, the historical record of numerous years of growth (juvenile and adult) may be examined, especially in long-lived species such as *N. tetricus*.

The answer to the second question will only be known when a greater range of species, with differing reproductive strategies have been examined. At present it appears that species with a non-dispersive larval phase, provided they are permanent reef residents,

are almost always resource limiting (Thresher 1983; Schmitt and Holbrook 1986), whereas in species with a dispersive larval phase the extent of resource limitation is less, but also highly variable between species and in space and time, and is not readily predicted by reproductive strategy. For example in the pomacentrids, a family with large eggs and parental egg care, in some species resource limitation in the form of available food appears to be an important factor determining growth (Jones 1990, Forrester 1990) and in others it is not (Pitcher 1992).

If the results of this research are applicable to most other temperate reef fishes having a dispersive larval stage, this could have important implications for the management of temperate reef fisheries. Classical fisheries theory predicts that in many cases unexploited stocks are resource limited, and it is the increase in productivity and recruitment arising from release from this limitation that is in part responsible for the ability of a fish stock to withstand fishing mortality (Ricker 1975). If natural populations of most temperate reef fishes are not usually resource limited, they may be particularly sensitive to exploitation, and any development of reef based fisheries should proceed with this in mind. A similar situation may exist with tropical reef species as the most recent studies, covering a range of species, suggest that the abundance and demography of reef fishes is mostly explained by variable recruitment, with no need to invoke density dependent processes after recruitment (Doherty and Fowler 1994; Williams *et al.* 1994).

While there is now a growing literature supporting direct recruitment-stock relationships in tropical reef species, there is, as yet, no evidence of a direct stock-recruitment relationship. Meekan *et al.* (1993) examined this possibility in the damselfish *Pomacentrus amboinensis*, and found that while reproduction influences recruitment timing, the magnitude of recruitment is largely determined within the plankton. If this finding is applicable to other reef species, both tropical and temperate, and post-recruitment growth and mortality is usually density independent, the most

appropriate management strategy for fisheries based on such species would be to set allowable catch levels according to measured annual recruitment strengths.

This investigation was instigated by my observation that isolated populations of a number of the species examined appeared to have considerably different size structures, and by the possibility that these differences were structured by varying levels of resource limitation. The results indicate that these isolated populations were not resource limiting, and instead, were probably structured by the spatial and temporal variability in recruitment that has been documented in numerous studies of reef fish demography (Doherty and Williams 1988a).

## **Chapter 7 Concluding Discussion**

### **7.1 Introduction**

While the fundamental aim of this thesis was to assess the importance of resource limitation to post-recruitment growth and the ecology of common temperate reef fishes, it was first necessary to investigate more basic aspects of the biology of the model species. These aspects were movement, growth, and reproduction, and an understanding of each of these aspects was an important prerequisite for a study investigating spatial and temporal patterns of growth. This basic work was necessary as very little is known of the biology of temperate Australasian reef fishes, and temperate reef fishes in general. This lack of knowledge applied to the six species investigated in this study, even though they rank amongst the most common and abundant resident reef fishes in southern Australian waters.

### **7.2 Movement**

In any study of the demography of fishes it is important to understand the role that movements can play, as post-recruitment movements over large spatial scales could explain much of the spatial variation in adult densities that has been observed in studies of temperate fish faunas (e.g. Choat and Ayling 1987). Such movements could also minimise the extent to which localised sources of mortality, and variation in resource availability, could structure an assemblage.

The results of this study indicate that for all species investigated, movement is restricted by habitat boundaries, such as depth or the reef-sand interface, and for most species is further restricted within a small home-range or territory. While such a result is predictable by extrapolation from the results of movement studies conducted on tropical reef fish (e.g. Reese 1973) it is still an important one, as the movement patterns of temperate reef fishes have received little attention (Jones 1988a). The results of the present study, and those of recent studies examining movements of other temperate reef



species (e.g. Jones 1984b; Davies and Anderson 1989; Matthews 1990) together suggest that many, if not the majority, of temperate species may be home-ranging. These home-ranges are relatively stable over the post-recruitment life of a fish, at least in locations not subject to extremes in environmental conditions.

In species with stable home ranges, populations would be susceptible to structuring by demographic processes, such as localised resource limitation and sources of mortality, as well as spatial and temporal variability in recruitment, occurring at a relatively small spatial scale. The magnitude of this scale would at least be at that of an individual reef, and perhaps considerably less, depending on reef size and the mobility of the species involved. This structuring would not occur to the same extent if fishes were highly mobile, as spatial patterns of abundance would be more likely to reflect variation in habitat quality, with fish moving to optimal locations. Such structuring, or microhabitat selection, has been shown to be one of the primary factors operating at a within-site scale ( $\leq 0.1 \text{ km}^2$ , Jones 1988a), with fish responding to variables such as topographic complexity (Ebeling *et al* 1980; Leum and Choat 1980), biogenic structure (Choat and Ayling 1987; DeMartini and Roberts 1990), current speed (Kingsford, 1980), threat of predation (Holbrook and Schmitt 1988a, 1988b), and depth (Holbrook *et al.* 1990).

As well as the demographic consequences that limited movements may have for natural populations of temperate reef fishes, there are also important consequences for populations subject to fishing mortality. As movements between reefs are likely to be restricted for many species, stocks on heavily fished reefs would be expected to be depleted rapidly, with little replenishment from adjacent areas. While the occurrence of a pelagic larval phase in most reef fishes ensures that localised stock depletions do not necessarily impact on recruitment levels, localised depletions can impact on the quality of fishing, particularly near resort areas where fishing effort is usually concentrated (e.g. Schaap and Green 1988). Management policies for such fisheries should be developed to limit fishing effort in areas where it is likely to become concentrated.

The restricted movements of reef fishes can be utilised in the creation of marine reserves, where a population is to be protected as a source of new recruits to adjacent fished areas or for conservation purposes. My results suggest that the design of these reserves could be optimised by choosing reserve sites with major habitat boundaries as their borders, thus restricting movements to adjacent fished areas.

The ability of such reserves to contain fishes is likely to have important consequences for future management of temperate reef fisheries. As reef fisheries are usually mixed fisheries, they are difficult to manage, given the large number of species involved and the low economic returns from most species. In tropical reef fisheries the cost of proper management and management research often exceeds the value of a fishery (Russ 1991). This situation undoubtedly applies to most temperate reef fisheries as well, and particularly in Tasmania where both recreational and professional fishermen are allowed to use gillnets, with few restrictions on where and when they may be set. By using the ability of a reserve to protect a proportion of the total population of target species, managers could at least allow for the provision of a buffer against recruitment overfishing caused by such practices, by ensuring a source of egg production was maintained.

### **7.3 Age and growth**

The longevity of the species examined in this study varied substantially, from less than 4 years in *Penicipelta vittiger*, to nearly 18 years in *Notolabrus fucicola*. The remaining species were intermediate in their lifespan, with *Meuschenia australis* living to 9 years, *Pictilabrus laticlavius* to 10 years, and *Pseudolabrus psittaculus* and *Notolabrus tetricus* to 11 years. A similar range in longevity is found in common northern temperate reef fishes, with surfperches (Embiotocidae) typically living for less than 5 years, and rockfishes (Scorpaenidae) capable of living for several decades (Holbrook *et al.* 1994). This variation in life expectancy has implications for the demography of reef fishes, as the temporal abundance of long-lived species such as *N. fucicola* may be far

more stable than short-lived species such as *P. vittiger*, due to buffering provided by multi-generational storage. This would be particularly the case where populations were primarily recruitment limited, and where recruitment success was temporally variable (Warner and Hughes 1988), a situation that appears to apply to many tropical reef species (Doherty and Williams 1988a, 1988b; Doherty 1994) and may also apply to many temperate ones as well.

While populations of short-lived species may lack the advantages of stability provided by multi-generational storage, this may be compensated for by other stabilising mechanisms, or simply be a consequence of, or adaptation to, living in an unstable environment. In the case of surfperch, temporal population stability is provided by a viviparous reproductive strategy, where fish give birth to large, non-dispersive juveniles; a strategy providing strong coupling between population size and resource availability (Holbrook *et al.* 1994). In the case of *P. vittiger*, a short lifespan may be the cost of the faster growth found in this species, with its concurrent relative advantage in fecundity over other fishes of a similar age, characteristics that may be important for the survival of a species living in an unstable environment. The optimal habitat of *P. vittiger* is shallow *Phyllospora comosa* forests growing in exposed waters, an unstable habitat in which mortality rates may often be high during storm events.

Of all the species investigated in this study, *P. vittiger* may be the species most at risk if it becomes the target or a by-catch of a reef fishery. This is because of the fast growth and short life-span of this species, as well as its susceptibility to capture in gillnets. The fast growth results in fish being of a sufficient size to be caught in nets before maturity is reached. This problem is compounded by the short life span which reduces the ability of the species to withstand several years of recruitment failure. In years of poor recruitment, the remaining population may be critical for rapid recovery, and the duration and magnitude of the recovery may be particularly sensitive to the levels of fishing effort during this time.

## 7.4 Reproduction

Unlike many coral reef fishes which spawn all year (Ehrlich 1975; Sale 1980), spawning of most temperate species is restricted to spring and summer (Jones 1988a, Ebeling and Hixon 1991), probably as a consequence of the greater planktonic productivity occurring during these seasons (Ebeling and Hixon 1991) which increases the availability of food to fish larvae. The species examined in this study appear to conform to this common pattern, with courting behaviour in all six species being observed from mid to late August through to late January; presumably this corresponds to the duration of spawning. This spawning pattern does not apply to all temperate species, however, and Moulton (1977) reported that 25% of species in Puget Sound spawned during autumn and winter. In temperate Australasian waters, fishes that spawn during this time include members of the family Cheilodactylidae (Thompson 1981), and some of these species, in particular *Cheilodactylus spectabilis*, rank amongst the most common reef residents in southern temperate waters.

For some species, the availability of a threshold abundance of plankton appears to be an important factor determining the survival of newborn larvae, and this threshold level may only be exceeded during brief transient pulses throughout the year (Thresher *et al.* 1989). It is this coincidence of spawning and food availability that forms the basis of the match/mismatch hypothesis of Cushing (1975), invoked to explain variation in recruitment strength. If such processes are important in the population dynamics of reef species in general, then by spawning over a protracted period, reef species, including those in this study, may maximise the possibility that at least some of their offspring are in the water column during conditions favourable to growth. Protracted spawning could also provide some protection against the impact of variability in other oceanic processes such as current strength and direction, processes that have been shown to advect some larvae away from conditions optimal for growth and reproduction (e.g. Choat *et al.* 1988; Holbrook *et al.* 1994), and that have been shown to be particularly variable in Tasmanian waters (Harris *et al.* 1987, 1991).

Both gonochoristic and hermaphroditic sexual systems were found amongst the fishes examined in this study. The monacanthids *Penicipelta vittiger* and *Meuschenia australis* are both gonochorists, a result that was expected as Thresher (1984) reported gonochorism to be the only sexual system recorded in tropical monacanthids and the related balistids. In the labrids, the situation is more complex, with variants of both sexual systems being found. *Notolabrus tetricus*, *pictilabrus laticlavius*, and *Pseudolabrus psittaculus* are monandric protogynous hermaphrodites, and *Notolabrus fucicola* is a secondary gonochorist. While both sexual systems have been reported for labrids, hermaphroditism is by far more common, and is the system used by most, if not all, tropical labrids (Thresher 1984), although it is less prevalent in temperate waters in northern Europe (Costello 1991).

In general, hermaphroditism is a common and highly successful reproductive strategy employed by fishes on both temperate and tropical reefs. In temperate Australasian waters, families with hermaphroditic representatives include the labrids, the related odacids, and the serranids. While the number of studies in which hermaphroditism in this region has been documented is limited (e.g. Jones 1980a, 1980b; Webb and Kingsford 1992), taxonomic studies and field guides indicate that most species within these families may be hermaphrodites (e.g. Thompson 1981; Gomon *et al.* 1994). In Tasmanian waters the hermaphroditic species include such common and abundant species as the odacids *Odax cyanomelas*, *Odax acroptilus*, *Neodax balteatus* and *Siponognathus beddomi*, the serranids *Caesioperca lepidoptera* and *C. rasor*, and the labrids *N. tetricus*, *P. laticlavius*, and *P. psittaculus*.

The proliferation of protogynous hermaphroditism in temperate reef species may have substantial implications for the proper management of fisheries based on these species, or in which they are an incidental by-catch. This would be particularly the case for species in which sex reversal is size or age based (Russ 1991), where removal of larger fishes may substantially alter the natural sex ratio (e.g. Thompson and Munroe 1983). In

a monandric protogynous hermaphrodite such as *Notolabrus tetricus*, a species which has recently become the focus of an intensive fishery, the removal of the larger males, coupled with the absence of initial phase males, could lead to a substantial decline in reproductive success. This decline would be in addition to that normally expected from the increase in mortality due to fishing, provided that sex reversal does not occur earlier in a fished population than in an undisturbed one.

Robertson (1972) has demonstrated that sex reversal in at least one labrid species is under social control, where removal of the males leads sex reversal in smaller fish. It is not yet clear to what extent this applies to other labrids, although there is evidence to suggest that in most species sex reversal may involve a degree of both developmental and social control (Thresher 1984). A similar spectrum of control mechanisms may apply in other temperate families such as the serranids and odacids, although, as with the labrids, this has yet to be documented. If fisheries are to develop around or impact on such potentially vulnerable species, more research should be focussed on both identifying hermaphroditic species, and determining the underlying mechanisms controlling sex reversal in them. This information would provide an additional benefit in that it could provide important clues about movement and distribution patterns of reef fishes (Webb and Kingsford 1992).

## **7.5 Spatial variability in growth**

A major aim of the work presented in this thesis was to test the assumption of Doherty and Williams (1988a) and others, that most populations of temperate reef fishes are not likely to be resource limited, at least for resources influencing growth. This work was precipitated by my observation that for most of the species examined here, isolated populations, sharing similar habitats, appeared to have substantially different size structures, and for the hermaphroditic species, different size at sex inversion, suggesting that they may represent a mosaic of populations experiencing different levels of resource limitation, primarily for those limiting growth. The results suggest that, in fact,

growth varies little between natural populations occupying similar habitats, either in space or in time, although for some species, nonspecific habitat effects can influence growth. The results support the assumption that growth in most natural open populations is not limited by resource availability, at least for resources influencing growth, although they provide no information on the extent to which other resources such as space may be important. There is evidence from a study examining the importance of resource availability to a community of temperate reef fishes, that neither food nor space are usually limiting (Stephens and Zerba 1981), results that may apply generally.

As Jones (1984b) has demonstrated that growth limitation can occur in the temperate labrid, *Notolabrus celidotus*, it is obvious that at least occasionally, resource limitation may occur in populations of reef fishes, and at times be an important demographic process. Further work involving a wider range of species, examining variability in fish growth in natural populations, in both space and time, is needed before the general applicability of Doherty and Williams (1988a,b) recruitment limitation model to temperate species can be properly assessed. However, empirical support for the applicability of this model to tropical reef fishes continues to grow (e.g. Doherty 1994), and it is unlikely that there would be any reason why this should not be so in the temperate zone as well, unless post-recruitment processes such as predation are particularly important in this zone in maintaining populations below the carrying capacity of their environment.

In temperate species with closed reproductive systems, such as the northern hemisphere surfperches, where most of the offspring are retained on the parental reef, resource limitation appears to be more important than recruitment limitation to population dynamics, with local resource availability explaining most variation in adult numbers (e.g. Holbrook and Schmitt 1986, 1989). A similar situation has been observed in a tropical species, *Acanthochromis polyacanthis*, where reproductive success is related to

resource availability (Thresher 1983, 1985). The extent to which populations of any particular species may be recruitment or resource limited may therefore be at least partly explained by the degree of parental investment in offspring, and extent, if any, of larval duration. Further studies are needed to examine the importance of early life history to the population dynamics of reef fishes, particularly research focussed on species such as clinids, many of which have been shown to display intermediate levels of parental care (e.g. Gunn and Thresher 1991).

The results of this study suggests differences in rates of growth cannot explain my initial observation that for many species the size structure of isolated populations differed substantially between locations with similar habitats. While the cause, or causes of this structuring awaits further investigation, it is apparent from the results of studies and reviews over the last decade, that populations of individual species can be highly variable in space and time (e.g. Holbrook *et al.* 1984), as a result of structuring processes operating before, during, and after recruitment. These processes can operate over small spatial scales and many of them could explain the observed variations in population structure.

The recruitment processes that have been found to cause structuring include recruitment variability (e.g. Doherty and Williams 1988a; Doherty 1994), habitat selection by recruits (e.g. Jones 1984, Carr 1991) and temporal variation in the availability of this habitat (Carr 1991). Post-recruitment processes include temporal variation in habitat availability (e.g. Holbrook *et al.* 1990a, 1990b), movements to preferred habitats or to spawning areas (e.g. Webb and Kingsford 1992), competition (e. g. Holbrook and Schmitt 1986, 1989), mortality due to storm events (Stephens *et al.* 1994), food limitation (Jones 1984b), shelter availability (Jones 1991) and predation (Hixon 1991). The importance of each of these processes, and others, is likely to vary substantially between different species of reef fish due to their heterogeneous array of life-histories,



as well as in space and time, particularly due to the interactive nature of all of these processes.

The results of this study, however, provide some support for the prediction by Doherty and Williams (1988a) that most species of temperate and tropical reef fishes with a dispersive larval stage rarely experience resource limitation, at least for an important resource such as food, which can influence rates of growth and mortality. Therefore, unless the predation effects suggested by Hixon (1991) are particularly important on temperate reefs, the patterns set by recruitment processes on temperate reefs may explain much of the observed variation in adult numbers at scales greater than the range of movements of individual fish, in a similar manner to that found for tropical reefs (Doherty 1994). Within the range of fish movement, movements in response to factors such as food, predation, shelter, and competition are likely to be the most important structuring mechanism.

Future research examining the population dynamics of temperate reef fishes with dispersive larvae needs to particularly concentrate on long-term studies examining the extent to which patterns of distribution and abundance at settlement are modified by post-recruitment processes. In particular, whether post-recruitment changes are due to movement or mortality, and if mortality is important in establishment of distributional patterns, the extent to which this is due to predation.

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